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BUCCAL FLOOR OF REPTILES, A SUMMARY

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ABSTRACT.— A general survey of the information presently available on the osteology and myology of the hyobranchial apparatus. Included in the survey are examples of the hyobranchial skeleton of the major groups of reptiles, including the Chelonia, Crocodilia, Rhynchocephalia, and Squamata. The myology treats the muscles directly associated with the hyoid as well as those associated with the functioning of the apparatus, but not arising or inserted directly on or from the hyoid. The innervation of the hyobranchial apparatus is reviewed and briefly discussed based on the information available in a few major studies. An attempt is made to cite all pertinent literature references, and in Tables 1 and 2 the references to basic areas are indicated. Twenty-nine plates and figures are included, some of which represent original research.

I. INTRODUCTION

Few anatomical areas have been subjected to such pronounced evolutionary changes as have the branchial apparatus and its derivatives in the vertebrate series. The hyoid apparatus has responded to these numerous adaptive changes with structural and functional modifications. One needs only to contemplate the change necessary in adapting from a structure bearing gills to one associated with lungs, from an immovable to a highly flexible tongue, or to the development of a larynx and archaic voice to appreciate the anatomical importance of this area. Furthermore, the class Reptilia consists of both primitive (turtles, crocodilians, and *Sphenodon*) and specialized (lizards and snakes) forms that include organisms possessing considerable structural diversification.

In reptiles the buccal floor consists of osseous and cartilaginous elements of the branchial skeleton and the associated connective and muscular tissues. Included among the

skeletal elements are the jaws, hyoid apparatus, laryngeal cartilages, and tracheal rings. The associated fleshy parts include the hyobranchial throat musculature, the tongue, and the nerves and blood vessels associated with them. There is also a variety of glands associated with the buccal floor; these are usually involved with the production of saliva that may be poisonous.

A complete comparative anatomical treatise on the buccal floor is not possible at this time, primarily because the necessary information is not available. Some anatomical studies on reptiles are precise and show considerable detail; however, the studies have too often been concerned primarily with one series of bones or one group of muscles rather than an entire anatomical pattern. As a result, we will confine our remarks to the present knowledge of the hyoid structure and associated muscles and nerves in the floor of the reptilian mouth. Many studies touch on the subject at hand in various ways. We have, therefore, included in the bibliography many

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studies not cited in the text. These have been useful in our examination of the materials available and are as follows: Adams 1919, 1925, Ashley 1955, Barrows and Smith 1947, Beddard 1905, Bellairs 1950, Bergman 1961, 1965, Boltt and Ewer 1964, Brock 1938, Bullcock and Tanner 1966, Byerly 1926, Chaine 1902, Chiasson 1962, Cowan and Hick 1951, Davis 1934, Duda 1965, Dullemeijer 1956, 1958, El Toubi 1938, 1947a, 1947b, El Toubi and Kalil 1952, Eyal-Giladi 1964, Evans 1955, Gandolfi 1908, Gans 1961, George 1948, George and Shad 1954, 1955, Haas 1952, 1960, 1968, 1973, Harris 1963, Heymans 1970, Iordansky 1970, Iyer 1942, 1943, Kamal, Hammouda, and Mokhtar 1970, Kesteven 1944, Kingman 1932, Kluge 1962, Kochva 1958, Liem, Marx, and Rabb 1971, Mahendra 1949, Malam 1941, McKay 1889, Minot 1880, Mivart 1867, Norris and Lowe 1951, Oldham, Smith, and Miller 1970, Parker 1880, Ping 1932, Presch 1971, Rathor 1969, Reese 1923, Rice 1920, Rieppel 1981, Rosenberg 1968, Sanders 1870, 1872, 1874, Schumacher 1956c, Sewertzoff 1929, Shah 1963, Sidky 1967, Siebenrock 1892a, 1892b, 1893, 1894, 1895, Sinitsin 1928, and Varkey 1979.

Tables 1 and 2 provide additional information on the material covered by these and other authors dealing with buccal floor and associated structures.

II. HYOID APPARATUS

General

The branchial skeleton, including the visceral arches, which we have associated with the more primitive gill-bearing vertebrates, has been recast in the tetrapods where its structure and function have been modified. The branchial skeleton now appears in tetrapods as a part of the skull; it includes the jaw and the hearing apparatus, as well as the larynx and trachial cartilage supports. The tetrapod has also retained the more central part of the old visceral skeleton, which is now known as the hyoid apparatus.

Because reptiles have lost the gill apparatus in all stages of development, the hyoid apparatus has assumed the function of a support for the tongue, glottis, and sometimes an extended dewlap. In modern reptiles, the

hyoid is composed of several osseous and cartilagenous elements and exhibits a variety of degrees of ossification. As a general rule, the larger (or older) the animal, the more ossified is the hyoid apparatus. In most reptiles, except in some snakes, the hyoid apparatus is a spreading, flexible structure that occupies space in, and forms a support for, most of the floor of the oropharynx.

Although the phylogenetic relationships of the hyoid apparatus and visceral arches are not completely understood, it is known that the hyoid apparatus is derived from the hyoid cartilage and the two succeeding arches. Romer (1956) believes that the hyoid of ancestral reptiles must have been more extensive and that traces of a third branchial cornu can be seen in some reptilian embryos. The third cornu is well demonstrated in monotreme mammals.

The nomenclature pertaining to the hyoid is not uniform. Furbringer (1922) describes the first two pairs of arches as the cornu hyale and the cornu brachiale I, respectively; the third arch is called the cornu brachiale II. This latter arch is referred to by Beddard (1907) as the branchial process and as the basibranchial by Gnanamuthu (1937). The third arch is seemingly absent in several reptiles, causing some workers to refer to the remaining two arches as the anterior and posterior cornua. Unfortunately, the identity of the third arch has not been clearly ascertained. The third arch may be a degenerate structure expressed as projections from the basihyoid or body of the hyoid, or it may be present as a separate arch with either the first or second arch being lost. In the Ophidia and some burrowing lizards such as *Anniella*, *Dibamus*, *Acontias*, *Acontophiops*, and *Typhlosaurus*, the hyoid is greatly reduced and the identity of the posterior cornua is not positively established. (See Rieppel 1981 for a more complete discussion.) A similar situation exists in the Testudines and Crocodilia. The development of the hyoid apparatus has been discussed by Rathke (1839), Kallius (1901), Howes and Swinnerton (1901), Peyer (1912), Edgeworth (1935), DeBeer (1937), Pringle (1954), El Toubi and Kamal (1959a,b), El Toubi and Majid (1961), Kamal and Hammouda (1965), Langebartel (1968), Rieppel (1981), and others (Table 1). These

| TABLE 1. Publications dealing with the buccal floor of reptiles. | | | | |
|--|---|-------------------------|---|---|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| Order Chelonia | | | | |
| Suborder Pleurodina | | | | |
| Pelomedusidae | | | | |
| <i>Pelusios</i> | | | Poglayan-Neuwall 1953 | Poglayan-Neuwall 1953 |
| Chelidae | | | | |
| <i>Batrochemys</i> | | | Poglayan-Neuwall 1953 | Poglayan-Neuwall 1953 |
| <i>Chelodina</i> | Furbringer 1922 | Winokur 1974 | Graper 1932 Kesteren 1944 Poglayan-Neuwall 1953 Shah 1963 | Kesteren 1944 Poglayan-Neuwall 1953 |
| Suborder Cryptodira | | | | |
| Dermatemydidae | | | | |
| <i>Dermatemys</i> | Furbringer 1922 | | | |
| Chelydridae | | | | |
| <i>Chelydra</i> | Furbringer 1922 Edgeworth 1935 Schumacher 1973 | Winokur 1974 | Camp 1923 Graper 1932 Poglayan-Neuwall 1953 Schumacher 1973 | Poglayan-Neuwall 1953 Soliman 1964 |
| <i>Kinosternon</i> | Furbringer 1922 Schumacher 1973 | | Poglayan-Neuwall 1953 Schumacher 1973 | Poglayan-Neuwall 1953 |
| <i>Sternotherus</i> | Furbringer 1922 Schumacher 1973 | | Poglayan-Neuwall 1953 Schumacher 1973 | Poglayan-Neuwall 1953 |
| Testudinidae | | | | |
| <i>Chrysemys</i> | Furbringer 1922 Ashley 1955 Schumacher 1973 | | Poglayan-Neuwall 1953 Ashley 1955 Schumacher 1973 | Poglayan-Neuwall 1953 |
| <i>Clemmys</i> | Siebenrock 1898 Furbringer 1922 Schumacher 1973 | | Graper 1932 Lubosch 1933 Schumacher 1973 | Lubosch 1933 Poglayan-Neuwall 1953 |
| <i>Cuora</i> | Furbringer 1922 | | Poglayan-Neuwall 1953 | Poglayan-Neuwall 1953 |
| <i>Deirochelys</i> | | | Shah 1963 | |
| <i>Dermatemys</i> | Furbringer 1922 | Winokur- Pers. Comm. | | |
| <i>Emys</i> | Walter 1887 Furbringer 1922 Schumacher 1973 | Sewentzoff 1929 | Walter 1887 Schumacher 1973 | Poglayan-Neuwall 1953 |
| <i>Gopherus</i> | | Winokur 1973 | George & Shad 1955 | |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|---|---|--------------------------------|---|---|
| <i>Graptemys</i> | | | Poglayen-Neuwall 1953 | Poglayen-Neuwall 1953 |
| <i>Geochelone</i> (<i>Testudo</i>) | Bojanus 1819 Furbringer 1922 Edgeworth 1935 Hacker & Schumacher 1955 Schumacher 1973 | Bojanus 1819 | Bojanus 1819 Graper 1932 Edgeworth 1935 Lubosch 1933 Poglayen-Neuwall 1953 Schumacher 1973 | Lubosch 1933 Poglayen-Neuwall 1953 |
| <i>Malachemys</i> | | | Poglayen-Neuwall 1953 | Poglayen-Neuwall 1953 |
| <i>Pseudemys</i> | Furbringer 1922 Schumacher 1973 | | Ashley 1955 Poglayen-Neuwall 1953 Schumacher 1973 | Poglayen-Neuwall 1953 |
| <i>Terrapene</i> | Furbringer 1922 | | Poglayen-Neuwall 1953 | Poglayen-Neuwall 1953 |
| Trionychidae | | | | |
| <i>Trionyx</i> (<i>Amyda</i>) | Siebenrock 1898 Sondhi 1958 Furbringer 1922 Schumacher 1973 | Sondhi 1958 | Graper 1932 Lubosch 1933 Poglayen-Neuwall 1953 Schumacher 1973 | Poglayen-Neuwall 1953 |
| <i>Lissemys</i> | Furbringer 1922 Sondhi 1958 Schumacher 1973 | Gnananuthu 1937 Sondhi 1958 | George & Shad 1954 Sondhi 1958 Schumacher 1973 | |
| Cheloniidae | | | | |
| <i>Caretta</i> | Furbringer 1922 Schumacher 1973 | | Poglayen-Neuwall 1953 Schumacher 1973 | Poglayen-Neuwall 1953 |
| Dermachelyidae | | | | |
| <i>Dermochelys</i> | Schumacher 1973 | | Poglayen-Neuwall 1953 Poglayen-Neuwall 1953/54 Schumacher 1973 | Poglayen-Neuwall 1953 Poglayen-Neuwall 1953/54 |
| Order Rhynchocephalia | | | | |
| Sphenodontidae | | | | |
| <i>Sphenodon</i> | Osawa 1898 Howes & Swinnerton 1901 Furbringer 1922 Edgeworth 1931,35 Rieppel 1978 | Sewertzoff 1929 | Osawa 1898 Camp 1923 Byerly 1926 Edgeworth 1931,35 Lightoller 1939 Kesteven 1944 Rieppel 1978 | Osawa 1898 Lubosch 1933 Kesteven 1944 Rieppel 1978 |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|------------------------|--|------------------------|--|-------------------------------|
| Order Squamata | | | | |
| Suborder Sauria | | | | |
| Gekkonidae | | | | |
| <i>Ascolabotes</i> | | Sewertzoff 1929 | Camp 1923 Edgeworth 1935 | |
| <i>Cnemaspis</i> | Richter 1933 | | | |
| <i>Coleonyx</i> | Camp 1923 Kluge 1962 | | Camp 1923 | |
| <i>Eublepharis</i> | Cope 1892 Camp 1923 | | | |
| <i>Gehrydra</i> | Richter 1933 | | | |
| <i>Gekko</i> | Camp 1923 Richter 1933 | | Camp 1923 Lubosch 1933 | Lubosch 1933 |
| <i>Gymnodactylus</i> | Richter 1933 | | Brock 1938 Kesteven 1944 | Kesteven 1944 |
| <i>Hemidactylus</i> | Zavattari 1908 Richter 1933 Edgeworth 1935 | Ping 1932 | Zavattari 1909 Ping 1932 Edgeworth 1935 Gnanamuthu 1937 | |
| <i>Phyllodactylus</i> | Cope 1892 | | | |
| <i>Platydictylus</i> | | | Sanders 1870 Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| <i>Ptychozoon</i> | Richter 1933 | | | |
| <i>Stenodactylus</i> | | | Gnanamuthu 1937 | |
| <i>Tarentola</i> | Richter 1933 | | Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| <i>Thecodactylus</i> | | | Kesteven 1944 | Kesteven 1944 |
| <i>Uroplatus</i> | Versluis 1898, 1904 Camp 1923 Edgeworth 1935 | | | |
| Dibamidae | | | | |
| <i>Dibamus</i> | Rieppel 1981 | | Gasc 1968 | |
| Iguanidae | | | | |
| <i>Amblyrhynchus</i> | Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Anolis</i> | Cope 1892 | | Kesteven 1944 | Willard 1918 Kesteven 1944 |
| <i>Basiliscus</i> | Zavattari 1908 | Gnanamuthu 1937 | Gnanamuthu 1937 | |
| <i>Brachylophus</i> | Camp 1923 Avery & Tanner 1971 | Avery & Tanner 1971 | Camp 1923 Avery & Tanner 1971 | |
| <i>Callisaurus</i> | Cox & Tanner 1977 | | Cox & Tanner 1977 | |
| <i>Chalarodon</i> | Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | Renous-Lecuru 1972 |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|----------------------|--|---|---|--|
| <i>Chamaeleolis</i> | Beddard 1907 | | | |
| <i>Conolophus</i> | Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Cophosaurus</i> | Cox & Tanner 1977 | | Cox & Tanner 1977 | |
| <i>Crotaphytus</i> | Cope 1892 Robison & Tanner 1962 | | Davis 1934 Robison & Tanner 1962 | |
| <i>Ctenosaura</i> | Oelrich 1951 Avery & Tanner 1971 | Oelrich 1956 Avery & Tanner 1971 | Oelrich 1956 Avery & Tanner 1971 | |
| <i>Cyclura</i> | Avery & Tanner 1971 | Gandolfi 1908 Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Dipsosaurus</i> | Cope 1892 Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Enyaliosaurus</i> | Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Holbrookia</i> | Cox & Tanner 1977 | | Cox & Tanner 1977 | |
| <i>Iguana</i> | Edgeworth 1935 Avery & Tanner 1971 Oldham & Smith 1975 | Gandolfi 1908 Avery & Tanner 1971 Oldham & Smith 1975 | Mivart 1867 Edgeworth 1935 Poglayan-Neuwall 1954 Avery & Tanner 1971 Oldham & Smith 1975 | Poglayan-Neuwall 1954 Oldham & Smith 1975 |
| <i>Liolaemus</i> | | Gandolfi 1908 | | |
| <i>Oplurus</i> | Avery & Tanner 1971 | Avery & Tanner 1971 | Avery & Tanner 1971 | |
| <i>Phrynosoma</i> | Cope 1892 Camp 1923 Richter 1933 Jenkins & Tanner 1968 | | Sanders 1874 Camp 1923 Jenkins & Tanner 1968 | |
| <i>Polychrus</i> | Richter 1933 | | | |
| <i>Sauromalus</i> | Avery & Tanner 1964, 1971 | Avery & Tanner 1971 | Avery & Tanner 1964, 1971 | |
| <i>Sceloporus</i> | Cope 1892 | | Secoy 1971 | |
| <i>Tropidurus</i> | Zavattari 1908 Edgeworth 1935 | | Zavattari 1908 Edgeworth 1935 | |
| <i>Uma</i> | Cox & Tanner 1977 | | Cox & Tanner 1977 | |
| <i>Urosaurus</i> | Fanghella, Avery & Tanner 1975 | | Fanghella, Avery & Tanner 1975 | |
| <i>Uta</i> | Fanghella, Avery & Tanner 1975 | | Fanghella, Avery & Tanner 1975 | |

| Table 1 continued. | | | | |
|-----------------------|--|---|--|--|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| Agamidae | | | | |
| <i>Agama</i> | Edgeworth 1935 El-Toubi 1947 Harris 1963 Eyal-Giladi 1964 | Gandolfi 1908 | DeVis 1883 Lubosch 1933 Edgeworth 1935 Poglayen-Neuwall 1954 Harris 1963 | Lubosch 1933 Poglayen-Neuwall 1954 Carpenter et al. 1977 |
| <i>Amphibolurus</i> | Richter 1933 | Gandolfi 1908 | Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| <i>Calotes</i> | Zavattari 1908 Camp 1923 Richter 1933 Edgeworth 1935 Iyer 1943 | Gandolfi 1908 Sewerteoff 1929 Gnanamuthu 1937 | Camp 1923 Gnanamuthu 1937 Poglayen-Neuwall 1954 | Gnanamuthu 1937 Poglayen-Neuwall 1954 |
| <i>Ceratophora</i> | Richter 1933 | | | |
| <i>Chlamydosaurus</i> | Beddard 1905 | | DeVis 1883 | Renous & Lecuru 1972 |
| <i>Cophotis</i> | Richter 1933 | | | |
| <i>Draco</i> | Richter 1933 | Gnanamuthu 1937 | Gnanamuthu 1937 | |
| <i>Hydrosaurus</i> | Richter 1933 | | | |
| <i>Leiolepis</i> | Richter 1933 | | Sanders 1872 Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| <i>Lyriocephalus</i> | Richter 1933 | | | |
| <i>Otocryptis</i> | Richter 1933 | | | |
| <i>Phrynocephalus</i> | Richter 1933 Kesteven 1944 | Sewertzoff 1929 | Kesteven 1944 | |
| <i>Physignathus</i> | Kesteven 1944 | | Kesteven 1944 | Kesteven 1944 |
| <i>Sitana</i> | | | Gnanamuthu 1937 | |
| <i>Uromastix</i> | Islam 1955 Tilak 1964a,b | | Furbringer 1922 Lubosch 1933 Edgeworth 1935 George 1948 Poglayen-Neuwall 1954 Throckmorton 1978 | Poglayen-Neuwall 1954 |
| Chamaeleonidae | | | | |
| <i>Chamaeleo</i> | Zavattari 1908 Edgeworth 1935 Gnanamuthu 1937 Jollie 1960 | Lubosch 1932 Gnanamuthu 1937 | Mivart 1870 Mivart 1876 Zavattari 1908 Camp 1923 Lubosch 1933 Edgeworth 1935 Gnanamuthu 1937 Kesteven 1944 Poglayen-Neuwall 1954 | Gnanamuthu 1937 Kesteven 1944 Poglayen-Neuwall 1954 |
| Scincidae | | | | |
| <i>Ablepharus</i> | | Sewertzoff 1929 | | |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|------------------------|--|--|--|---|
| <i>Chalcides</i> | Richter 1933 El Toubi 1938 El Toubi & Kamal 1959a,b | | | Soliman & Hegazy 1971 |
| <i>Eumeces</i> | Cope 1892 Zavattari 1908 Richter 1933 Nash & Tanner 1970 | | Zavattari 1908 Edgeworth 1935 Nash & Tanner 1970 | |
| <i>Lygosoma</i> | Richter 1933 | | | |
| <i>Mabuya</i> | Richter 1933 Gnanamuthu 1937 Tao & Ramaswami 1952 | Gnanamuthu 1937 | Gnanamuthu 1937 | |
| <i>Nessia</i> | Richter 1933 | | | |
| <i>Riopa</i> | Richter 1933 | | | |
| <i>Scincus</i> | Richter 1933 | | | |
| <i>Tiligua</i> | Beddard 1907 | | Lightoller 1939 Kesteven 1944 Poglayan-Neuwall 1954 | Lightoller 1939 Poglayan-Neuwall 1954 |
| <i>Trachysaurus</i> | Beddard 1907 | | Poglayan-Neuwall 1954 | Poglayan-Neuwall 1954 |
| <i>Typhlosaurus</i> | Rieppel 1981 | | | |
| Cordylidae | | | | |
| <i>Cordylus</i> | Beddard 1907 Camp 1923 Richter 1933 Edgeworth 1935 | | Camp 1923 Edgeworth 1935 | |
| <i>Gerrhosaurus</i> | Camp 1923 | | Camp 1923 | |
| <i>Zonrus</i> | Camp 1923 | | | |
| Lacertidae | | | | |
| <i>Acanthodactylus</i> | Richter 1933 | | | |
| <i>Cabrita</i> | | Gnanamuthu 1937 | Gnanamuthu 1937 | |
| <i>Lacerta</i> | Walter 1887 Zavattari 1908 Richter 1933 Edgeworth 1935 | Sewertzoff 1929 | Walter 1887 Camp 1923 Edgeworth 1935 Poglayan-Neuwall 1954 | Poglayan-Neuwall 1954 |
| <i>Ophisops</i> | Richter 1933 | | | |
| Teiidae | | | | |
| <i>Ameiva</i> | Richter 1933 Fisher & Tanner 1970 | Minot 1880 Sewertzoff 1929 Presch 1971 | Poglayan-Neuwall 1954 Fisher & Tanner 1970 | Poglayan-Neuwall 1954 |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|-----------------------|---|---|---|--|
| <i>Cnemidophorus</i> | Cope 1892 Fisher & Tanner 1970 | Presch 1971 | Poglayen-Neuwall 1954 Fisher & Tanner 1970 | Poglayen-Neuwall 1954 |
| <i>Neusticurus</i> | Richter 1933 | | | |
| <i>Tupinambis</i> | Zavattari 1908 Reese 1932 Edgeworth 1935 Jollie 1960 | | Zavattari 1908 Camp 1923 Edgeworth 1935 Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| Anguinidae | | | | |
| <i>Anguis</i> | Richter 1933 | Sewertzoff 1929 | | |
| <i>Gerrhonotus</i> | Walter 1887 Cope 1892 | | Camp 1923 Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| <i>Ophiosaurus</i> | Walter 1887 | Sewertzoff 1929 | Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| Xenosauridae | | | | |
| <i>Shinosaurus</i> | McDowell & Bogart 1954 | McDowell & Bogart 1954 | Haas 1960 | |
| <i>Xenosaurus</i> | Camp 1923 McDowell & Bogart 1954 | McDowell & Bogart 1954 | Camp 1923 Haas 1960 | |
| Helodermatidae | | | | |
| <i>Heloderma</i> | Cope 1892 McDowell & Bogart 1954 | McDowell & Bogart 1954 | Camp 1923 Poglayen-Neuwall 1954 | Poglayen-Neuwall 1954 |
| Varanidae | | | | |
| <i>Varanus</i> | Richter 1933 McDowell & Bogart 1954 Sondhi 1958 | Sewertzoff 1929 McDowell & Bogart 1954 Sondhi 1958 | Bradley 1903 Camp 1923 Edgeworth 1935 Gnanamuthu 1937 Lightoller 1939 Kesteven 1944 Poglayen-Neuwall 1954 Sondhi 1958 | Watkinson 1906 Lightoller 1939 Kesteven 1944 Poglayen-Neuwall 1954 |
| Lanthanotidae | | | | |
| <i>Lanthanotus</i> | McDowell & Bogart 1954 McDowell 1972 Rieppel 1981 | McDowell & Bogart 1954 | | |
| Anniellidae | | | | |
| <i>Anniella</i> | Cope 1892 Rieppel 1981 | | Camp 1923 | |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|---------------------------|---|------------|--|------------------|
| Amphisbaenidae | | | | |
| <i>Amphisbaena</i> | Camp 1923 Richter 1933 Jollie 1960 | | Smalian 1885 Camp 1923 | |
| <i>Anopsibaena</i> | | | Smalian 1885 | |
| <i>Bipes</i> | | | Renous 1977 Smalian 1885 | |
| <i>Blanus</i> | | | Smalian 1885 | |
| <i>Monopeltis</i> | Richter 1933 | | | |
| <i>Rhineura</i> | Cope 1892 | | Camp 1923 | |
| <i>Trogonophis</i> | | | Smalian 1885 | |
| Xantusidae | | | | |
| <i>Xantusia</i> | Savage 1963 Cope 1892 | | Camp 1923 | |
| Suborder Serpentes | | | | |
| Anomalepididae | | | | |
| <i>Anomalepis</i> | Smith & Warner 1948 | | Haas 1968 | |
| <i>Helminthophis</i> | List 1966 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Liotyphlops</i> | List 1966 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| Typhlopidae | | | | |
| <i>Typhlops</i> | List 1966 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Typhlophis</i> | Evans 1955 List 1966 | Evans 1955 | Evans 1955 | |
| Leptotyphlopidae | | | | |
| <i>Leptotyphlops</i> | Smith & Warner 1948 List 1966 Langebartel 1968 Oldham, Smith & Miller 1970 | | Langebartel 1968 Oldham, Smith & Miller 1970 | Langebartel 1968 |
| Uropeltidae | | | | |
| <i>Platyplectrurus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Plectrurus</i> | Rieppel 1981 | | | |
| <i>Rhinophis</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Silybura</i> | Langebartel 1968 | | | |
| <i>Uropeltis</i> | | | Langebartel 1968 | Langebartel 1968 |

| Table 1 continued. | | | | |
|----------------------|---|------------------|---|---|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| Aniliidae | | | | |
| <i>Anilius</i> | Smith & Warner 1948 Langebartel 1968 Rieppel 1981 | | Langebartel 1968 | Langebartel 1968 |
| <i>Cylindrophis</i> | Smith & Warner 1948 Langebartel 1968 | | Lubosch 1933 Langebartel 1968 | Lubosch 1933 Langebartel 1968 |
| Xenopeltidae | | | | |
| <i>Xenopeltis</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| Boidae | | | | |
| <i>Aspidites</i> | Smith & Warner 1948 Langebartel 1968 | | | |
| <i>Boa</i> | Langebartel 1968 | | Gibson 1966 | |
| <i>Calabaria</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Charina</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Chondropython</i> | Langebartel 1968 | | | |
| <i>Constrictor</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Enygrus</i> | Langebartel 1968 | | | |
| <i>Epicrates</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Eryx</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Eunectes</i> | Langebartel 1968 | | Anthony & Serra 1950 Langebartel 1968 | Langebartel 1968 |
| <i>Liasis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Lichanura</i> | Langebartel 1968 | Hershkowitz 1941 | | |
| <i>Loxocemus</i> | Smith & Warner 1948 Langebartel 1968 | | | |
| <i>Nardoana</i> | Langebartel 1968 | | | |
| <i>Python</i> | Furbringer 1922 Langebartel 1968 Oldham, Smith & Miller 1970 | | Lubosch 1933 Edgeworth 1935 Kesteven 1944 Frazzetta 1966 Langebartel 1968 Oldham, Smith & Miller 1970 | Lubosch 1933 Kesteven 1944 Langebartel 1968 |
| <i>Sanzinia</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Trachyboa</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |

| Table 1 continued. | | | | |
|-----------------------|--|-------------------------|---|--|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| Colubridae | | | | |
| <i>Achalinus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Achrochordus</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Adelphicus</i> | Langebartel 1968 | | | |
| <i>Amblycephalus</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Aparallactus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Apostolepis</i> | Langebartel 1968 | | | |
| <i>Atretium</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Boiga</i> | Langebartel 1968 | | | |
| <i>Carphophis</i> | Smith & Warner 1948 Langebartel 1968 | | | |
| <i>Cerberus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Chersodromus</i> | Langebartel 1968 | | | |
| <i>Chersydrus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Chrysopelea</i> | Langebartel 1968 | | | |
| <i>Clelia</i> | Langebartel 1968 | | | |
| <i>Coluber</i> | Walter 1887 Langebartel 1968 | | Walter 1887 | |
| <i>Coniophanes</i> | Langebartel 1968 | | | |
| <i>Conophis</i> | Langebartel 1968 | | | |
| <i>Conepsis</i> | Langebartel 1968 | | | |
| <i>Crotaphopeltis</i> | Langebartel 1968 | | | |
| <i>Cyclagras</i> | Langebartel 1968 | | | |
| <i>Dasypeltis</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Dendrophidion</i> | Langebartel 1968 | | | |
| <i>Diadophis</i> | Langebartel 1968 | | | |
| <i>Dipsadotoa</i> | Langebartel 1968 | | | |
| <i>Dispholidus</i> | Langebartel 1968 | | | |
| <i>Dromophis</i> | Langebartel 1968 | | | |
| <i>Drymarchon</i> | Langebartel 1968 | | | |
| <i>Drymobius</i> | Langebartel 1968 | | | |
| <i>Dryophis</i> | Langebartel 1968 | | Lubosch 1933 | |
| <i>Elaphe</i> | Langebartel 1968 | Morgans & Heidt 1978 | Albright & Nelson 1959 Langebartel 1968 | Langebartel 1968 Auen & Langebartel 1977 |
| <i>Elapomorphus</i> | Langebartel 1968 | | | |
| <i>Elapops</i> | Langebartel 1968 | | | |

| Table 1 continued. | | | | |
|-----------------------|--|--|---|---------------------------------|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| <i>Enhydrus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Enulius</i> | Langebartel 1968 | | | |
| <i>Farancia</i> | Langebartel 1968 | | | |
| <i>Ficimia</i> | Langebartel 1968 | | | |
| <i>Fimbrios</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Geophis</i> | Langebartel 1968 | | | |
| <i>Haldca</i> | Langebartel 1968 | | | |
| <i>Haplopeltura</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Heterodon</i> | Weaver 1965 Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Homalopsis</i> | Langebartel 1968 | | | |
| <i>Lampropeltis</i> | Langebartel 1968 | | | |
| <i>Leptodeira</i> | Langebartel 1968 | | | |
| <i>Leptophis</i> | Langebartel 1968 | | | |
| <i>Manolepis</i> | Langebartel 1968 | | | |
| <i>Masticophis</i> | Langebartel 1968 | | | |
| <i>Mehelya</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Natrix</i> | Sondhi 1958 | Sondhi 1958 | Sondhi 1958 | Sondhi 1958 |
| <i>Nerodia</i> | Langebartel 1968 Oldham, Smith & Miller 1970 | Morgans & Heidt 1978 Varkey 1979 | Langebartel 1968 Oldham, Smith & Miller 1970 Varkey 1979 | Langebartel 1968 Varkey 1979 |
| <i>Ninia</i> | Langebartel 1968 | | | |
| <i>Nothopsis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Ophiodrys</i> | Langebartel 1968 Cundall 1974 | | Cundall 1974 | |
| <i>Oxybelis</i> | Langebartel 1968 | | | |
| <i>Oxyrhabdiniun</i> | Langebartel 1968 | | | |
| <i>Pituophis</i> | Smith & Warner 1948 Bullock & Tanner 1966 Langebartel 1968 Oldham, Smith & Miller 1970 | | Oldham, Smith & Miller 1970 | |
| <i>Psamnodynastes</i> | Langebartel 1968 | | | |
| <i>Rhadineae</i> | Langebartel 1968 | | | |
| <i>Rhadinella</i> | Langebartel 1968 | | | |
| <i>Rhinocheilus</i> | Langebartel 1968 | | | |
| <i>Salvadora</i> | Langebartel 1968 | | | |
| <i>Sibynomorphus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Sonora</i> | Langebartel 1968 | | | |
| <i>Tantilla</i> | Langebartel 1968 | | | |

| Table 1 continued. | | | | |
|----------------------|--|-----------------|--|--|
| Genus | Hyoid | Tongue | Musculature | Nerves |
| <i>Thamnophis</i> | Bullock & Tanner 1966 Langebartel 1968 Oldham, Smith & Miller 1970 | | Langebartel 1968 Oldham, Smith & Miller 1970 | Langebartel 1968 Aven & Langebartel 1977 |
| <i>Toluca</i> | Langebartel 1968 | | | |
| <i>Trimorphodon</i> | Langebartel 1968 | | | |
| <i>Tropidonotus</i> | Langebartel 1968 | Sewertzoff 1929 | Lubosch 1933 | Lubosch 1933 |
| <i>Xenodermus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Xenodon</i> | Weaver 1965 | | Anthony & Serra 1949 Langebartel 1968 | Langebartel 1968 |
| Elapidae | | | | |
| <i>Acanthophis</i> | Langebartel 1968 | | | |
| <i>Aspidelaps</i> | Langebartel 1968 | | | |
| <i>Bungarus</i> | Langebartel 1968 | | | |
| <i>Calliophis</i> | Langebartel 1968 | | | |
| <i>Demansia</i> | Langebartel 1968 | | | |
| <i>Dendrospis</i> | Langebartel 1968 | | | |
| <i>Denisonia</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Doliophis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Elaps</i> | Langebartel 1968 | | | |
| <i>Elapsoidea</i> | Langebartel 1968 | | | |
| <i>Furina</i> | Langebartel 1968 | | | |
| <i>Hemachatus</i> | Langebartel 1968 | | | |
| <i>Hemibungarus</i> | Langebartel 1968 | | | |
| <i>Leptomicrurus</i> | Langebartel 1968 | | | |
| <i>Maticora</i> | Langebartel 1968 | | | |
| <i>Micruroides</i> | Langebartel 1968 | | | |
| <i>Micrurus</i> | Smith & Warner 1948 Langebartel 1968 | | | |
| <i>Naja</i> | Langebartel 1968 Kamal, Hamouda & Mokhtar 1970 | | Lubosch 1933 Langebartel 1968 | Langebartel 1968 |
| <i>Notechis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Ogmodon</i> | Langebartel 1968 | | | |
| <i>Pseudechis</i> | | | Kesteven 1944 | Kesteven 1944 |
| <i>Pseudelaps</i> | Langebartel 1968 | | | |
| <i>Ultocalamus</i> | Langebartel 1968 | | | |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|-------------------------|---|-----------------|---|---|
| Hydrophidae | | | | |
| <i>Aipysurus</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Hydrophis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Kerilia</i> | Langebartel 1968 | | | |
| <i>Lapemis</i> | Smith & Warner 1948 Langebartel 1968 | | | |
| <i>Laticauda</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Pelamis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Thalasophina</i> | Langebartel 1968 | | | |
| Viperidae | | | | |
| <i>Aspis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Atheris</i> | Langebartel 1968 | | | |
| <i>Atractaspis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Bitis</i> | Langebartel 1968 | | | |
| <i>Causus</i> | Langebartel 1968 | | Haas 1952 Langebartel 1968 | Langebartel 1968 |
| <i>Cerastes</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Echis</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Pseudocerastes</i> | Langebartel 1968 | | | |
| <i>Vipera</i> | Furbringer 1922 Langebartel 1968 | | Edgeworth 1935 Langebartel 1968 | Langebartel 1968 |
| Crotalidae | | | | |
| <i>Agkistrodon</i> | Smith & Warner 1948 Langebartel 1968 | | Langebartel 1968 Kardong 1973 | Langebartel 1968 |
| <i>Bothrops</i> | Langebartel 1968 | | Langebartel 1968 | Langebartel 1968 |
| <i>Crotalus</i> | Langebartel 1968 Oldham, Smith & Miller 1970 | | Langebartel 1968 Oldham, Smith & Miller 1970 | Langebartel 1968 |
| <i>Lachesis</i> | Langebartel 1968 | | Lubosch 1933 Langebartel 1968 | Lubosch 1933 Langebartel 1968 |
| <i>Sistrurus</i> | Langebartel 1968 | | | |
| <i>Trimeresurus</i> | Langebartel 1968 | | | |
| Order Crocodilia | | | | |
| Crocodylidae | | | | |
| <i>Alligator</i> | Reese 1915 Furbringer 1922 Edgeworth 1935 Chiason 1962 | Sewertzoff 1929 | Reese 1915 Lubosch 1933 Edgeworth 1935 Chiason 1962 Poglayen-Neuwall 1953b | Reese 1915 Lubosch 1933 Poglayen-Neuwall 1953b |
| <i>Caiman</i> | Schumacher 1973 | | Schumacher 1973 | Schumacher 1973 |

Table 1 continued.

| Genus | Hyoid | Tongue | Musculature | Nerves |
|-------------------|--|--------------------------------|--|--|
| <i>Crocodylus</i> | Furbringer 1922 Sondhi 1958 Frank & Smit 1974 | Sewertzoff 1929 Sondhi 1958 | Camp 1923 Edgeworth 1935 Kesteven 1944 Sondhi 1958 Poglayen-Neuwall 1953b | Kesteven 1944 Poglayen-Neuwall 1953b |
| Gavialidae | | | | |
| <i>Gavialis</i> | Furbringer 1922 Sondhi 1958 | Sondhi 1958 | Sondhi 1958 | Sondhi 1958 |

attempts have not led to a completely satisfactory understanding of the hyoid derivatives, and the homologies of the hyoid constituents cannot be ascertained without comparative embryological information on the development of the reptiles' buccal floor. Thus, our interpretation of the hyoids of reptiles should be considered tentative at best.

The tentativeness of our present understanding of the homologies of many of these structures, when considered for the reptiles as a whole, is indicated in a recent study by Frank and Smit (1974). They consider the early ontogeny of the columella auris of *Crocodylus niloticus*, and its relationship to the reptilian hyoid arch is reviewed and discussed in detail. Considerable effort is expended in the clarification of terms and in the description of particular morphological structures that have been in some confusion as a result of misunderstandings. Frank and Smit (1974) were trying to establish a model to be used, and to stimulate subsequent research. We hope that such studies will be undertaken and will clarify structural homologies for each of the remaining arches occurring in reptiles. Ontogenetic studies leading to an understanding not only of reptiles in general but also of each reptilian order are needed before we can consistently assign exact anatomical limits to structures and provide an appropriate name for each morphological entity. Until such are available, however, we must remain within the limits of our present knowledge.

The hyoid apparatus of reptiles has been described by Romer (1956) as having a median ventral piece, the copula, which forms the body of the hyoid (= corpus hyoideum BH). Extending anteriorly from the corpus hyoideum is a medial process, the processus

lingualis (= processus entoglossus PL), which terminates in the substance of the tongue. Laterally the corpus gives off three paired horns or cornua that extend posterodorsally around the throat, ending freely or attached to the stapelial structures. The anteriormost pair of cornua are the hyoid cornua (HC), which, at their distal ends, articulate with the most lateral of the hyoid bars or epihyals (EH). The second pair of cornua are elongated bars (usually cartilagenous) forming the first ceratobranchials (CBI) and attaching distally to the epihyals by way of short cartilaginous bars on each side of the first epibranchials (EBI). The third and last processes of the corpus hyoideum are a pair of posteriorly extending rods, the second epibranchials (EBII), a pair of short cartilaginous bars that articulate by their distal ends with the epibranchials of the first and second arches (Figs. 1-3).

The association of the hyoid with, and its attachment to, the skull is of evolutionary importance. In primitive lizards, such as some Gekkonidae, the hyoid is attached to the extracolumella. Thus the hyoid apparatus maintains its association with the stapelial structures that may be derived from its dorsal extremities. This point of union is or is not persistent as indicated by Versluys (1898 and 1904) and, in some individuals, is transferred to the paraoccipital process of the opisthotic bone.

The possession of all three cornua is considered the primitive condition and is demonstrated in *Sphenodon*, where all the cornua are long, slender, and well-developed structures. A few gekkos and xantusiids have an incomplete third arch with a slight break between ceratobranchial II and epibranchial II. In the Iguanidae (Avery and Tanner 1971) all

three arches are present, but lack their distal connections in some cases.

Rhynchocephalia

The hyoid of *Sphenodon* has been discussed by Osawa (1898, Howes and Swinnerton 1901, Furbringer 1922, Edgeworth 1931, 1935, and Rieppel 1978).

The hyoid apparatus of *Sphenodon* (Fig. 1) is simple with all elements present. The basihyoid is broad with a short lingual process extending anteriorly. Laterally the basihyoid extends as projections corresponding to the hyoid cornua but not distinctly separate from the basihyoid. At their distal ends, the cornua articulate with epihyals that extend straight posteriorly. The basihyoid also has a pair of posterior projections, the second ceratobranchials, that are widely separated and curve laterally at their distal ends. The first ceratobranchials articulate with the basihyoid lateral to the point of origin of the second ceratobranchials. They curve and closely approach the distal ends of the epihyals. Rieppel (1978) illustrated the hyoid apparatus and its associated muscles. A taxonomic survey provides a general overview of this order:

Chelonia

The hyoid apparatus of turtles has been described by the following:

Chelidae

Chelodina (Furbringer 1922)

Dermatemydidae

Dermatemys (Furbringer (1922)

Chelydridae

Cheydra (Furbringer 1922, Edgeworth 1935, Schumacher 1973), *Kinosternon* (Furbringer 1922, Schumacher 1973), *Sternotherus* (Furbringer 1922, Schumacher 1973), *Chrysemys* (Furbringer 1922, Ashley 1955, Schumacher 1973), *Cuora* (Furbringer 1922), *Clemmys* (Siebenrock 1898, Furbringer 1922, Schumacher 1973), *Emys* (Walter 1887, Furbringer 1922, Schumacher 1973), *Geochelone* (Bojanus 1819, Furbringer 1922, Edgeworth 1935, Schumacher 1973), *Terrapene* (Furbringer 1922).

Trionychidae

Lissemys (Furbringer 1922, Sondhi 1958, Schumacher 1973), *Trionyx* (Siebenrock 1898, Sondhi 1958, Furbringer 1922, Schumacher 1973).

Cheloniidae

Caretta (Furbringer 1922, Schumacher 1973).

Dermochelyidae

Dermochelys (Schumacher 1973).

Schumacher (1973) has treated the hyoids of turtles and crocodilians extensively in this series, so our discussion will serve as a general review.

The hyoid apparatus of turtles has been described briefly by Bojanus (1819) and figured by Mitchell and Morehouse (1863). More

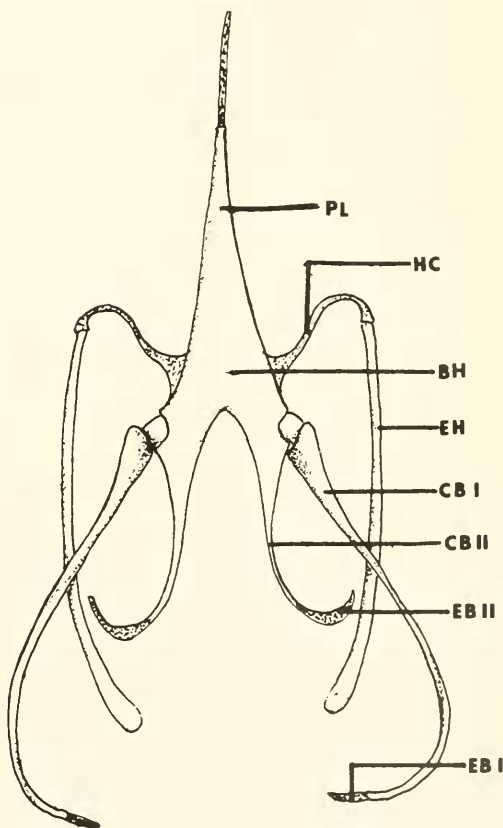


Fig. 1. Hyoid apparatus of *Sphenodon punctatum* (USUN 029429): BH-body of hyoid, (basihyoid) CB1-first ceratobranchial, CB11-second ceratobranchial, EB1-first epibranchial, EB11-second epibranchial, EH-epihyal, HC-hyoid cornu, PL-processus lingualis.

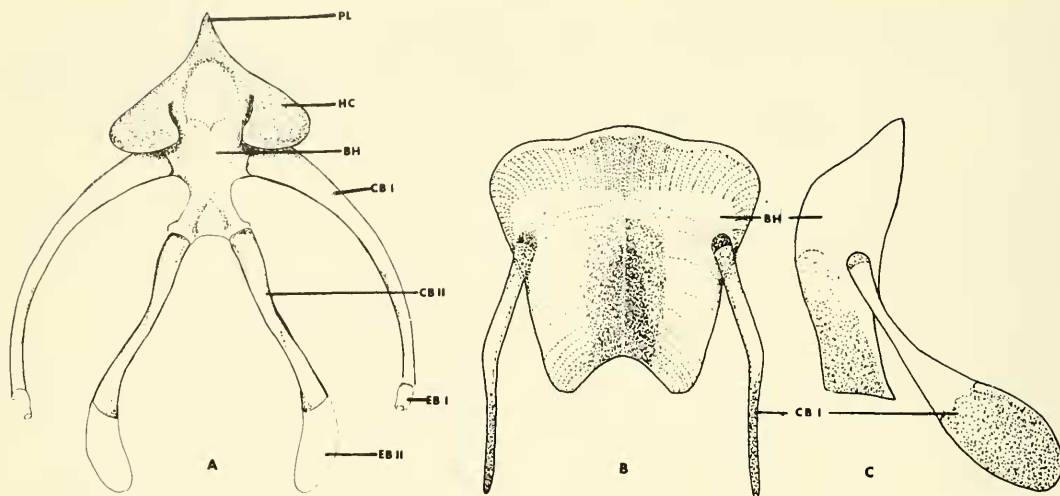


Fig. 2.—Hyoid apparatus of A, *Chelydra serpentina* (Southern Connecticut State College, 598), ventral view; B, *Caiman sclerops*, ventral view; C, *Caiman sclerops*, lateral view (SCSC 585).

complete reports include those of Siebenrock (1898), Furbringer (1922), Versluys (1936), Gnanamuthu (1937), and Sondhi (1958). The hyoid is more ossified than that of most lizards and snakes.

In *Trionyx* and *Lissemys* the hyoid has a body with a lingual process equipped with a hypoglossum (Sondhi 1958); this is a leaflike plate of cartilage loosely attached to its ventral side. The hyoid cornua are greatly reduced and form knoblike projections from the body. The second ceratobranchials extend posteriorly from the body as subcylindrical structures.

The body of the hyoid is composed of three pairs of serially arranged cartilaginous blocks. The most anterior part has on its lateral margins very short anterior projections. The middle pair of plates bear the articulating surfaces for the hyoid cornua. The posterior pair of plates are completely fused to the middle pair and have between them and the middle plates a diamond-shaped interspace. Posteriorly the last pair of plates provides facets for the articulations of the second ceratobranchials. In *Chelydra* the hyoid is more solidly constructed, consisting of bone except for its anterior end, the ceratohyals, and the epihyals, which are cartilage (Fig. 2 A).

The possession of a hypoglossum by turtles appears to be unique. The structure was first described by Stannius (1856) as an entoglos-

sum. The term *hypoglossum* was first used by Furbringer (1922), who described it as the part not entering the tongue. Nick (1913) and Versluys (1936) observed that in turtles, with the exception of *Dermochelys*, the hypoglossum is platelike, unpaired, and lies ventral to the lingual process. Nick (1913) also suggests that the hypoglossum is a chondrification of connective tissue of the tendinous plate. The hypoglossum is extensive in *Trionyx*, in which it may have two slender posterior strips or be an elongate plate, rounded at each end and extending anteriorly from the middle components of the body of the hyoid almost to the symphysis of the mandible. Sondhi (1958) suggested that the hypoglossum functions to raise or lower the buccal floor by means of two muscles (Mm. entoglosso-hypoglossalis and hypoglosso-lateralis) attached to its dorsal surface and extending to the processus entoglossus and the buccal floor. In other genera, *Chelydra*, *Chrysemys*, *Pseudemys*, and *Sternotherus*, it is proportionally smaller and varies in shape (Fig. 3). Hacker and Schumacher (1955) figure it for *Testudo* and describe the M. entoglosso-glossus that serves as an attachment between the hypoglossum and the processus lingualis. In *Gopherus agassizi*, the hypoglossum is elongate and slender with a median ridge ventrally and a convexity dorsally. It is closely associated with the processus lingualis. A paired muscle (M. entoglosso-glossus) is attached to its dorsal surface on

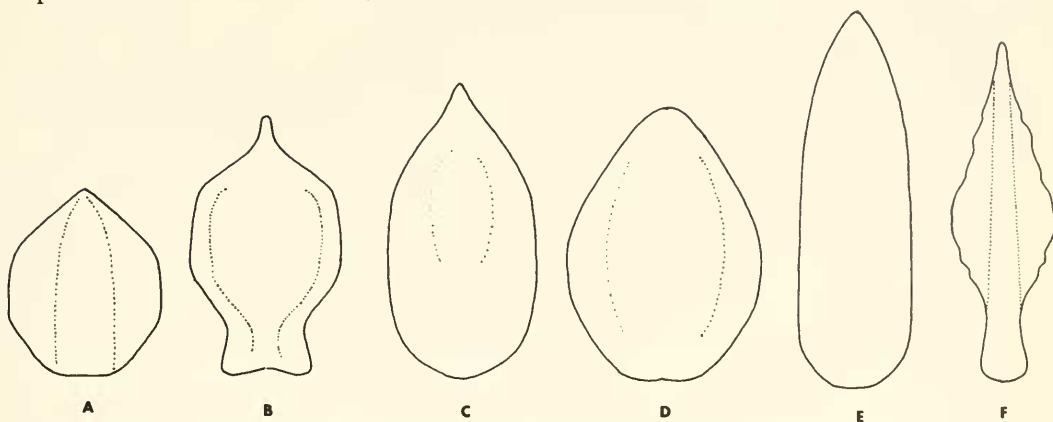


Fig. 3. The hypoglossum of five genera of turtles, ventral views: A, *Chrysemys picta* (SCSC 602); B, *Sternotherus odoratus* (SCSC 476); C, *Pseudemys scripta* (BYU 40343); D, *Chelydra serpentina* (BYU 33642); E, *Trionyx spinifera* (SCSC 596); F, *Gopherus agassizi* (BYU 30084).

each side, just lateral to the median concavity. These muscles extend dorsally and anteriorly to insert in the connective tissues surrounding the processus lingualis. The pointed anterior end of the hypoglossum extends beyond the end of the processus lingualis.

In the few examples we have seen, the hypoglossum of terrestrial tortoises appears to be more slender and with better developed muscular attachments to the hyoid apparatus than in other turtles.

The hyoid cornua are short cartilaginous knobs covered ventrally by the *M. ceratohyoideum*. The first ceratobranchials are long, subcylindrical, rodlike bones that articulate with the middle component of the body of the hyoid. They extend posteriorly to curve dorsally and partially surround the neck, where they lie embedded in the *M. ceratohyoideus*.

The second ceratobranchials are composed of proximal bony parts and distal cartilaginous parts. The distal ends girdle the posterior part of the neck and lie beneath the *M. omohyoideum*. A ligament connects the base of each second ceratobranchial with the anterior part of each hyoid cornu.

Crocodylia

In *Alligator*, *Crocodylus*, and *Gavialis* the hyoid apparatus consists of the body of the hyoid and a pair of posterior projections. The hyoid cornua and all other processes are absent. Sondhi (1958) has described the structures in *Gavialis* in detail. The body of the hyoid is the most prominent part of the appa-

ratus and forms an inverted triangular cartilaginous plate. There is a deep notch in the posterior margin, and laterally it bears a facet for the articulation of the posterior projection. The hyoid lies dorsal to the *M. mylohyoideus*, ventral to the glottis, and anterior to part of the trachea. Anteriorly the body is covered in part by the *Mm. hyoglossus* and *genioglossus*. The posterior projections are rodlike, cartilaginous, and extend posteromedially, gradually becoming flattened, compressed, and twisted. A ligament connects these projections with fused rodlike structures closely adhering to the posterolateral borders of the body and probably corresponding to the second ceratobranchials of other reptiles.

The above description of *Gavialis* corresponds to our findings in *Caiman* except that the body of the hyoid of the latter is not triangular, but broadly rectangular and, from a dorsal view, similar to a wide-bladed shovel (Fig. 2-B,C). There is a shallow notch posteriorly, and the posterior projections are bone proximally and expand into flat sheets of cartilage distally. We did not find a ligament extending dorsolaterally onto the cervical area from the ends of the posterior projections.

Lacertilia

The hyoid of lizards has been examined by the following:

Gekkonidae

Cnemaspis (Richter 1933), *Coleonyx* (Camp 1923, Kluge 1962), *Eublepharis*

TABLE 2. Publications, not previously cited, dealing with topics peripheral to the buccal floor.

A. Osteology

1. Chelonia

- Ashley 1955, *Chelydra*, *Chrysemys*
 Coppert 1903, *Testudo*

2. Rhynchocephalia

- Coppert 1900, *Sphenodon*
 Lakjer 1927, *Sphenodon*
 Rieppel 1979, 1981, *Sphenodon*

3. Lacertila

- Barrows and Smith 1947, *Xenosaurus*
 Beddard 1905a, *Uromastix*
 Bellairs 1950, *Anniella*
 Criley 1968, *Barisia*, *Elgaria*, *Gerrhonotus*
 Duda 1965, *Agama*
 El Toubi 1938, *Scincus*
 El Toubi 1947a, *Agama*
 El Toubi 1947b, *Uromastix*
 El Toubi and Kamal 1959a, *Chalcides*
 El Toubi and Kamal 1959b, *Chalcides*
 Elyal-Giladi 1964, *Agama*, *Chalcides*
 George 1954, *Uromastix*
 Coppert 1903, *Amphisbaena*, *Calotes*, *Cnemidophorus*, *Lacerta*, *Mabuia*, *Platydictylus*
 Iyer 1942, *Calotes*
 Iyer 1943, *Calotes*
 Kingman 1932, *Eumeces*
 Lakjer 1927, *Ameiva*, *Anguis*, *Amphisbaena*, *Calotes*, *Chalcides*, *Chamaelo*, *Cordylus*, *Eumeces*, *Gekko*, *Hyperodapedon*, *Heloderma*, *Iguana*, *Lialis*, *Lygosoma*, *Phrynosoma*, *Pygopus*, *Lacerta*, *Tiligua*, *Trogonophis*, *Uromastix*, *Varanus*
 Mahendra 1949, *Hemidactylus*
 Malam 1941, *Gerrhosaurus*
 Norris and Lowe 1951, *Phrynosoma*
 Parker 1880, *Lacerta*, *Agama*
 Rathor 1969, *Ophiomorus*
 Rice 1920, *Eumeces*
 Siebenrock 1892a, *Uroplatus*
 Siebenrock 1892b, *Scincus*
 Siebenrock 1893, *Brookesia*
 Siebenrock 1894, *Lacerta*
 Siebenrock 1895, *Agama*
 Sinitsin 1928, *Alopoglossus*, *Ameiva*, *Anadia*, *Bachia*, *Callopiastes*, *Cercosaura*, *Centropyx*, *Cnemidophorus*, *Dracaena*, *Dicrodon*, *Echinosaura*, *Ecleopus*, *Euspondylus*, *Gymnophthalmus*, *Iphisa*, *Leposoma*, *Neusticurus*, *Ophiognomon*, *Pantodactylus*, *Pleonodactylus*, *Pholidobolus*, *Pructoporus*, *Scolecosaurus*, *Teius*, *Tretioscincus*, *Tupinambis*
 Tilak 1964a, *Uromastix*
 Toerien 1950, *Anniella*
 Webb 1951, *Oedura*, *Palmatogecko*
 Weiner and Smith 1965, *Crotaphytus*
 Young 1942, *Xantusia*
 Zangerl 1944, *Amphisbaena*, *Bipes*, *Geocalamus*, *Leptosternon*, *Monopeltis*, *Rhineura*, *Trogonophis*

Table 2 continued.

4. Ophidia

- Berman 1961, *Echis*, *Vipera*
 Berman 1965, *Calamaria*
 Bolt and Ewer 1954, *Bitis*
 Dullemeijer 1956, *Vipera*
 Dullemeijer 1959, *Bitis*, *Crotalus*, *Trimeresurus*, *Vipera*
 Kardong 1974, 1977, *Agkistrodon*
 Liem, Mark and Rabb 1971, *Azemiops*
 Coppert 1903, *Python*, *Tropidonotus*
 McKay 1889, *Acanthrophis*
 Rosenberg 1968, *Bungarus*
 Varkey 1979, *Nerodia*

5. Crocodilia

- Chiasson 1962, *Alligator*
 Coppert 1903, *Crocodylus*

B. Myology

1. Chelonia

- Adams 1919, *Chelydra*
 Ashley 1955, *Chelydra*, *Chrysemys*
 Schumacher 1956, *Amyda*, *Chelodina*, *Chelonia*, *Caretta*, *Clemmys*, *Dogania*, *Emydura*, *Emys*, *Eretmochelys*, *Graptemys*, *Hardella*, *Macrochelys*, *Hydromedusa*, *Pelomedusa*, *Pelusios*, *Platyternon*, *Podocnemis*, *Testudo*, *Trionyx*
 Shah 1963, *Chelodina*, *Deirochelys*

2. Rhynchocephalia

- Adams 1919, *Sphenodon*
 Rieppel 1978, *Sphenodon*

3. Lacertila

- Adams 1919, *Iguana*, *Varanus*
 Bradley 1903, *Agama*, *Gekko*, *Lacerta*, *Pseudopus*, *Varanus*
 Brock 1938, *Gymnodactylus*
 Davis 1934, *Crotaphytus*
 George 1948, *Uromastix*
 Iordansky 1970, *Agama*, *Cordylus*, *Eumeces*, *Gekko*, *Lacerta*, *Ophiosaurus*, *Teratoscincus*, *Varanus*
 Norris and Lowe 1951, *Phrynosoma*
 Rathor 1969, *Ophiomorus*
 Tornier 1904, *Chamaeleo*

4. Ophidia

- Adams 1925, *Natrix*
 Bergman 1961, *Echis*, *Vipera*
 Bergman 1965, *Calamaria*
 Bolt and Ewer 1954, *Bitis*
 Cowan and Hick 1951, *Thamnophis*
 Dullemeijer 1956, *Vipera*
 Dullemeijer 1959, *Bitis*, *Crotalus*, *Trimeresurus*, *Vipera*
 Haas 1930, *Amblycephalus*, *Calbaria*, *Calamaria*, *Cylindrophis*, *Eryx*, *Ilysia*, *Oxybelis*, *Silybura*, *Xenopeltis*
 Haas 1931a, *Acrochordus*, *Amblycephalus*, *Atractaspis*, *Atractus*, *Bungarus*, *Calabar*, *Calamaria*

Table 2 continued.

- maria, Causus, Cerberus, Chersydrus, Cylin-
drophis, Dasypeltis, Dispsadomophus, Elaps,
Eryx, Glauconia, Ilysia, Lachesis, Leptognathus,
Naja, Oxybelis, Pelamis, Python, Poly-
odontophis, Silyura, Typhlops, Xenodon,
Xenopeltis
Haas 1931b, *Acrodordus*, *Atractaspis*, *Causus*, *Cer-
berus*, *Chersydrus*, *Cylindrophis*, *Dasypeltis*,
Dispholidus, *Leptognathus*, *Petalognathus*, *Poly-
odontophis*, *Scaphiophis*, *Xenodon*
Haas 1952, *Causus*
Heymans 1970, *Natrix*
Heymans 1975, *Aparallactus*, *Atractaspis*,
Chilorhinophis
Kochva 1958a, *Vipera*
Kochva 1958b, *Agkistrodon*, *Aspis*, *Atheris*, *Atrac-
taspis*, *Bitis*, *Bothrops*, *Causus*, *Crotalus*, *Echis*,
Natrix, *Naja*, *Ophiophagus*, *Pseudocerastes*, *Vi-
pera*, *Walterinnesia*
Kardong 1974, *Agkistrodon*
Liem, Mark, and Rabb 1971, *Azemiops*
McKey 1889, *Acanthrophis*
Rosenberg 1968, *Bungarus*
Rosenberg and Gans 1976, *Elachistodon*
5. *Crocodylia*
Adams 1919, *Alligator*
Chiasson 1962, *Alligator*
- C. Miscellaneous
1. *Chelonina*
Johnson 1922, Branchial pouch derivatives, *Che-
lydra*, *Chrysemys*
Goppert 1900, *Larynx*, *Chelonina*, *Dermochelys*,
Emys, *Testudo*
Siebenrock 1900, *Larynx*, *Testudo*
2. *Lacertila*
Goppert 1900, *Larynx*, *Amphisbaena*, *Platydac-
tylus*, *Tiliqua*
Perrier 1902, Thymus and thyroid glands, *Lacerta*
Saint-Remy and Prenant 1904, Thymus and thy-
roid glands, *Anguis*, *Lacerta*
Sidkey 1967, Carotid Sinus, *Chalcides*, *Scincus*
3. *Ophidia*
Goppert 1900, *Larynx*, *Coronella*, *Python*,
Tropidonotus
Kroll 1973, Taste buds, *Leptotyphlops*
Saint-Remy and Prenant 1904, Thymus and thy-
roid glands, *Coluber*, *Tropidonotus*
Van Bourgondien and Bother 1969, Cephalic arte-
rial patterns, *Agkistrodon*, *Crotalus*, *Lachesis*,
Sistrurus
4. *Crocodylia*
Goppert 1900, *Larynx*, *Crocodylus*
Siebenrock 1899, *Larynx*, *Crocodylus*

(Cope 1892, Camp 1923), *Gekko* (Camp 1923, Richter 1933), *Gehyra* (Richter 1933), *Gymnodactylus* (Richter 1933), *Hemidactylus* (Zavattari 1908, Richter 1933, Edgeworth 1935), *Phyllodactylus* (Cope 1892), *Ptychozoon* (Richter 1933), *Tarentola* (Richter 1933), *Uroplatus* (Versluys 1898, 1904, Camp 1923, Edgeworth 1935).

Dibamidæ

Dibamus (Rieppel 1981).

Iguanidæ

Amblyrhynchus (Avery & Tanner 1971), *Anolis* (Cope 1892), *Basiliscus* (Zavattari 1908), *Brachylophus* (Camp 1923, Avery & Tanner 1971), *Callisaurus* (Cox & Tanner 1977), *Chalarodon* (Avery & Tanner 1971), *Chamaeleolis* (Beddard 1907), *Conolophus* (Avery & Tanner 1971), *Cophosaurus* (Cox & Tanner 1977), *Crotaphytus* (Cope 1892, Robison & Tanner 1962), *Ctenosaura* (Oelrich 1956, Avery & Tanner 1971), *Cyclura* (Avery & Tanner 1971), *Dipsosaurus* (Cope 1892, Avery & Tanner 1971), *Enyaliosaurus* (Avery & Tanner 1971), *Holbrookia* (Cox & Tanner 1977), *Iguana* (Edgeworth 1935, Avery & Tanner 1971, Oldham & Smith 1945), *Oplurus* (Avery & Tanner 1971), *Phrynosoma* (Cope 1892, Camp 1923, Richter 1933, Jenkins & Tanner 1968), *Polychrus* (Richter 1933), *Sauromalus* (Avery & Tanner 1964, 1971), *Sceloporus* (Cope 1892), *Tropidurus* (Zavattari 1908, Edgeworth 1935), *Uma* (Cox & Tanner 1977), *Urosaurus* (Fanghella, Avery & Tanner 1975), *Uta* (Fanghella, Avery & Tanner 1975).

Agamidæ

Agama (Edgeworth 1935, El Toubi 1947, Harris 1963, Eyal-Giladi 1964), *Amphibolurus* (Richter 1933), *Calotes* (Zavattari 1908, Camp 1923, Richter 1933, Edgeworth 1935, Iyer 1943), *Ceratophura* (Richter 1933), *Chlamydosaurus* (Beddard 1905), *Cophotis* (Richter 1933), *Draco* (Richter 1933), *Hydrosaurus* (Richter 1933), *Leiolepis* (Richter 1933), *Lyrziocephalus* (Richter 1933), *Otocryptis* (Richter 1933), *Phrynocephalus* (Richter 1933, Kesteven 1944), *Physignathus* (Kes-

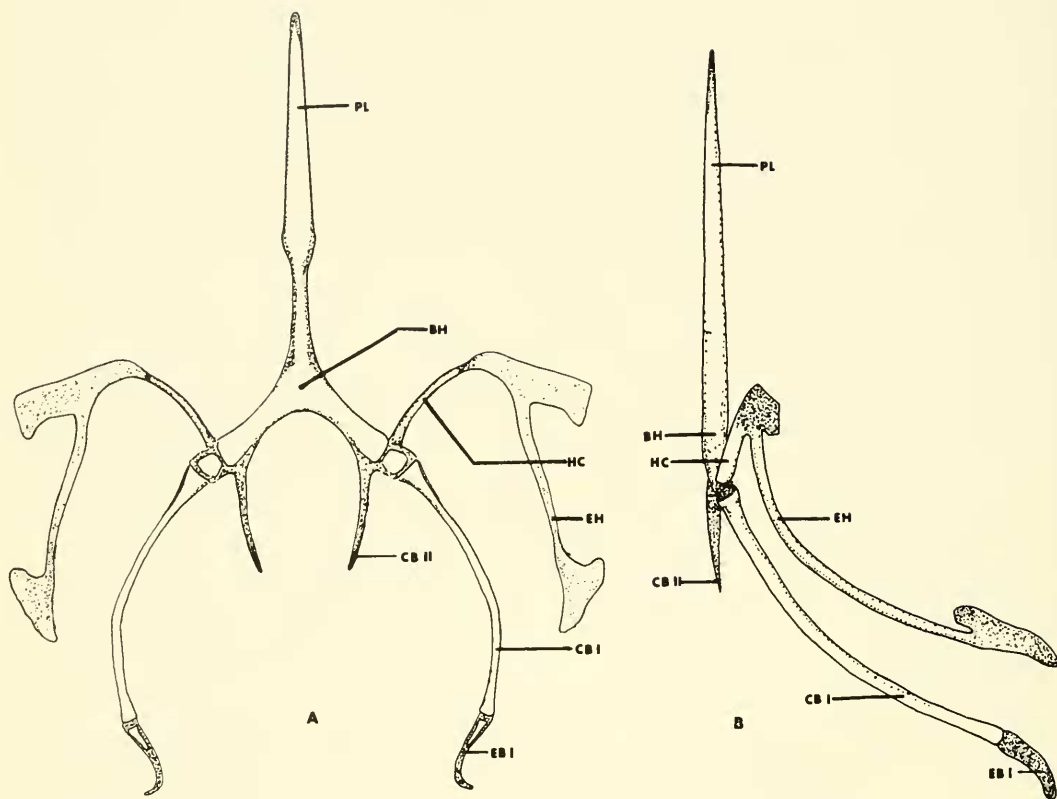


Fig. 4. Hyoid apparatus of *Tarentola annularis* (BYU 18123): A, ventral view; B, lateral view.

teven 1944), *Uromastix* (Islam 1955, Tilak 1964a,b).

Chamaeleonidae

Chamaeleo (Zavattari 1908, Edgeworth 1935, Gnanamuthu 1937, Jollie 1960).

Scincidae

Acontias (Rieppel 1981), *Acontophiops* (Rieppel 1981), *Chalcides* (Richter 1933, El Toubi 1938, El Toubi & Kamal 1959a,b), *Eumeces* (Cope 1892, Zavattari 1908, Richter 1933, Nash & Tanner 1970), *Lygosoma* (Richter 1933), *Mabuya* (Richter 1933, Gnanamuthu 1937, Rao & Ramaswami 1952), *Nessia* (Richter 1933), *Riopa* (Richter 1933), *Tiliqua* (Beddard 1907), *Scincus* (Richter 1933), *Trachysaurus* (Beddard 1907), *Typhlosaurus* (Rieppel 1981).

Cordylidae

Cordylus (Beddard 1907, Camp 1923, Richter 1933, Edgeworth 1935), *Gerrho-*

saurus (Camp 1923), *Zonurus* (Camp 1923).

Lacertidae

Acanthodactylus (Richter 1933), *Lacerta* (Walter 1887, Zavattari 1908, Richter 1933, Edgeworth 1935), *Ophisops* (Richter 1933).

Teiidae

Ameiva (Richter 1933, Fisher & Tanner 1970), *Cnemidophorus* (Cope 1892, Fisher & Tanner 1970), *Neusticurus* (Richter 1933), *Tupinambis* (Zavattari 1908, Reese 1932, Edgeworth 1935, Jollie 1960).

Anguinidae

Anguis (Richter 1933), *Gerrhonotus* (Walter 1887, Cope 1892), *Ophiosaurus* (Walter 1887).

Xenosauridae

Shinosaurus (McDowell & Bogert 1954), *Xenosaurus* (McDowell & Bogert 1954, McDowell 1972).

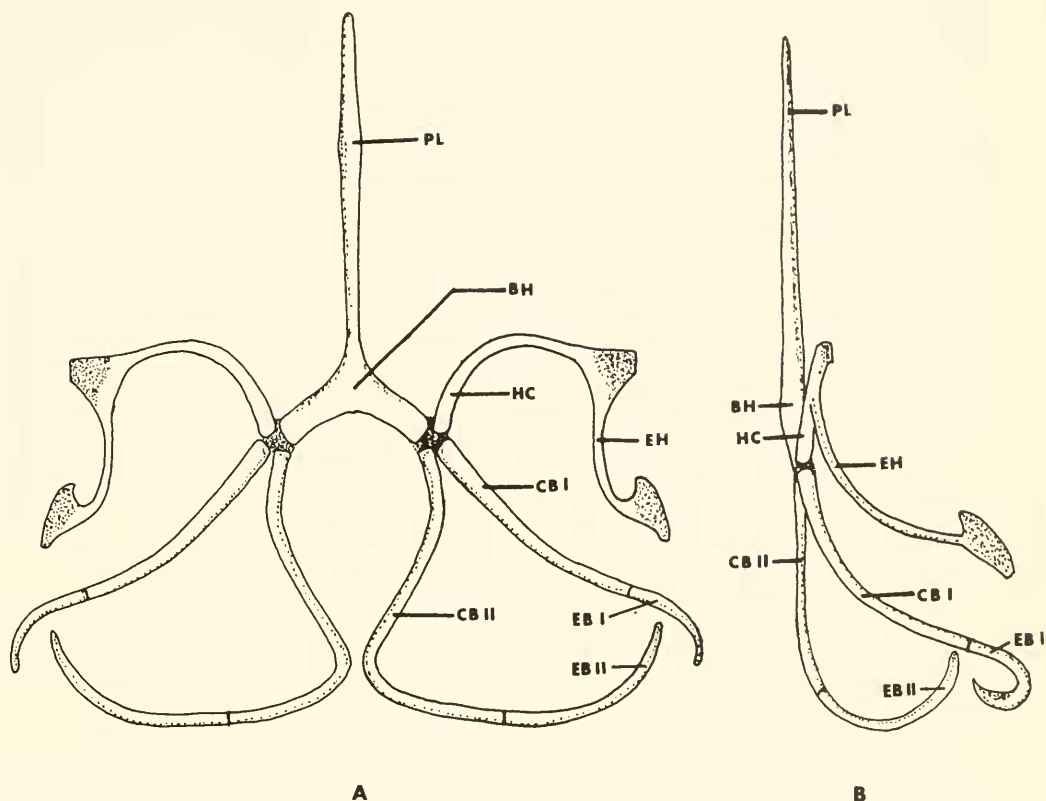


Fig. 5. Hyoid apparatus of *Coleonyx variegatus* (BYU 18796): A, ventral view; B, lateral view.

Helodermatidae

Heloderma (Cope 1892, McDowell & Bogert 1954).

Varanidae

Varanus (Richter 1933, McDowell & Bogert 1954, Sondhi 1958).

Lanthanotidae

Lanthanotus (McDowell & Bogert 1954, Rieppel 1981).

Anniellidae

Anniella (Cope 1892, Rieppel 1981).

Anphisbaenidae

Amphisbaena (Camp 1923, Richter 1933, Jollie 1960), *Monopeltis* (Richter 1933), *Rhineura* (Cope 1892).

Xantusiidae

Xantusia (Cope 1892, Savage 1963).

Most lizards have a hyoid consisting of a basihyal (corpus hyoideum) with a pair, each,

of anterior and posterior cornua as described by Cope (1892), Zavattari (1908), Furbringer (1922), Camp (1923), Versluys (1936), DeBeer (1937), Gnanamuthu (1937), Mahendra (1947), Rao and Ramaswami (1952), McDowell and Bogert (1954), Oelrich (1956), Romer (1956), Sondhi (1958), Jollie (1960), Robison and Tanner (1962), Avery and Tanner (1964), Jenkins and Tanner (1968), Fisher and Tanner (1970), Nash and Tanner (1970), Avery and Tanner (1971), Rieppel (1981), and others. For the remainder of this discussion we will use the hyoid nomenclature followed by Romer (1956) as described earlier. The hyoids of the geckos *Coleonyx*, *Gekko*, *Aristelliger*, *Hemidactylus*, *Phyllodactylus*, *Thecadactylus*, and *Eublepharis* have been described, and we figure *Tarentola* (Fig. 4) and *Coleonyx* (Fig. 5). In most, the body of the hyoid is small and slender, with a long rodlike lingual process extending anteriorly. A pair of hyoid cornua extend laterally; in

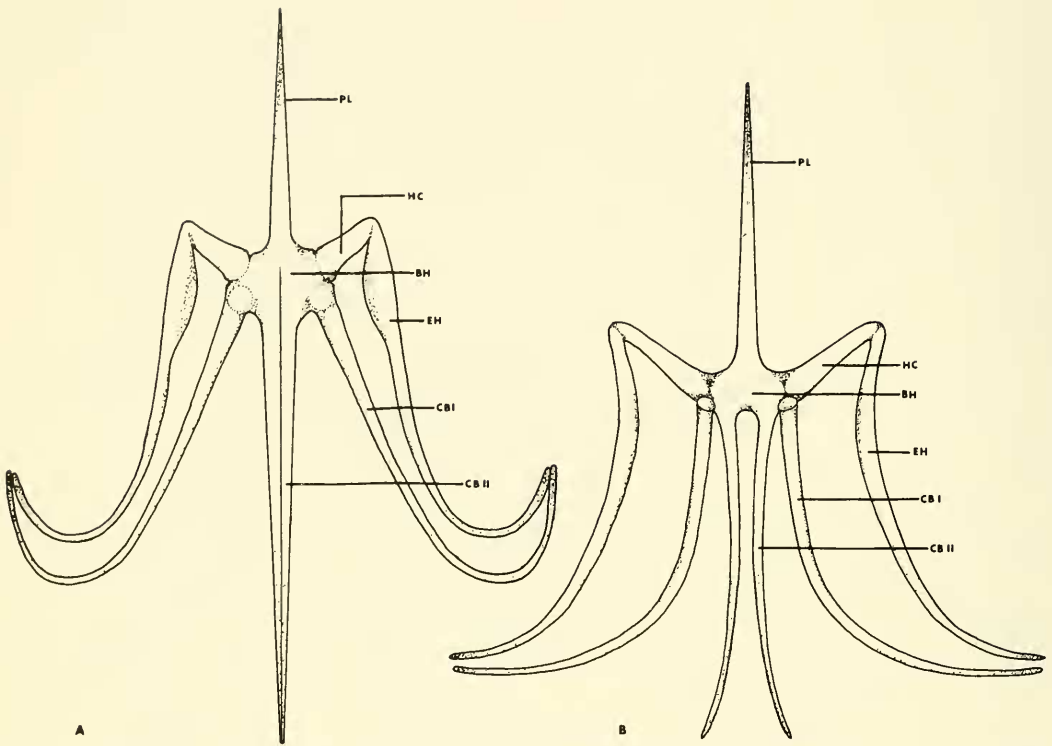


Fig. 6. Hyoid apparatus, ventral views: A, *Brachylophus brevicephalus* (BYU 32663); B, *Sauromalus obesus* (BYU 21728).

some species these form sigmoid curves, and in others they are straight rods. Articulating with the distal extremes of the hyoid cornua are the epihyals. Extending posteriorly from the body of the hyoid as a pair of short or long rods are the second ceratobranchials. A third set of arches, the first ceratobranchials, articulate at the point of attachment between the hyoid cornua and the body. The basic pattern is retained throughout the Gekkota, with some variation in the shape of the hyoid cornua; also, the first ceratobranchials, epihyals, or both may be lost in some genera.

In the Dibamidae, Rieppel (1981) has described the hyoid of *Dibamus* as having a posteriorly bifurcated basihyal with an elongated entoglossal process. The bony first ceratobranchials that articulate with the posterolateral limbs of the basihyal are shorter in *Dibamus* as compared to *Anniella*. He indicates a major specialization exists in that there are a pair of cartilaginous rods that support the aditus laryngis and approach but do not fuse to the posterolateral limbs of the

basihyal. These he considers to be hypohyals (hyoid cornua of Romer).

The hyoids of the iguanine lizards *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, and *Sauromalus* and Malagache iguanids *Chalarodon* and *Oplurus* have been investigated by Avery and Tanner (1971). Because these lizards possess all three arches of the hyoid apparatus, they are considered primitive (Fig. 6-A). The body of the hyoid (basihyal) is triangular in all the above genera except *Oplurus* and *Sauromalus*, in which it forms a broad flattened sheet of cartilage. In all the genera the hyoid cornu (hypohyal) is short and stout; it extends out from the body of the hyoid at right angles or projects slightly anterior to the body. Posterior to the body, the second ceratobranchials extend along the trachea and, in all genera except *Oplurus* and *Sauromalus*, lie close together. In the latter two genera the second ceratobranchials are widely separated by the bulk of the trachea (Fig. 6-B). In none of the genera are the sec-

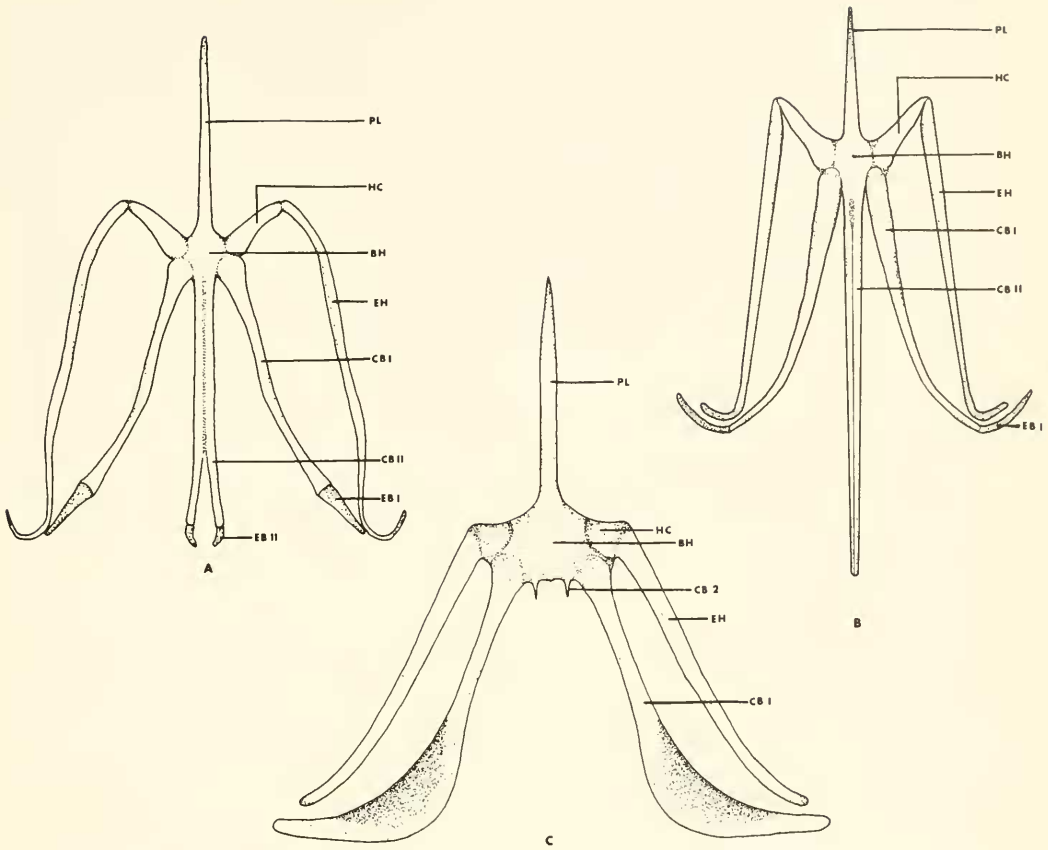


Fig. 7. Hyoid apparatus, ventral views: A, *Sceloporus magister* (BYU 30310); B, *Holbrookia maculata* (BYU 15752); C, *Phrynosoma platyrhinos* (BYU 22830).

ond ceratobranchials attached distally to the other arches. In some genera, particularly *Iguana*, the distal extremes of these processes attach to the skin and provide support for movement of the dewlap.

The first ceratobranchials articulate proximally with the body of the hyoid between the origins of the second ceratobranchials and the hyoid cornua. They are elongated, thin rods that taper to points distally and curve dorsolaterally to the sides of the neck, where they articulate with the epihyals (ceratohyals). The epihyals articulate between the hyoid cornua and the first ceratobranchials and form the most lateral extensions of the hyoid apparatus. At their proximal ends the epihyals are expanded into bladelike processes that extend medially toward the hyoid body. These processes are not developed to any degree in *Chalarodon* and *Oplurus*. Among the other iguanids studied and de-

scribed by one of us are the hyoids of *Crotaphytus*, *Holbrookia*, *Phrynosoma*, and *Uta*. We figure *Sceloporus magister* and *Holbrookia maculata* (Figs. 7-A & B) as representatives of the sceloporine genera. The basic pattern described in the iguanines is maintained with the following exceptions. In *Phrynosoma* the second ceratobranchials are greatly reduced, and the first ceratobranchials and epihyals are noticeably thickened (Fig. 7-C); the basihyoid is a laterally extended plate. *Anolis* has an exceptionally elongated hyoid apparatus, with the second ceratobranchials extending posteriorly along the midline forming approximately two-thirds the length of the entire hyoid apparatus. This anatomical development is associated with the functional dewlap (Fig. 8).

In the agamids, the following were examined: *Agama* (Duda 1965, Hass 1973), and Figure 9; *Calotes*, *Draco*, and *Sitana* (Gnana-

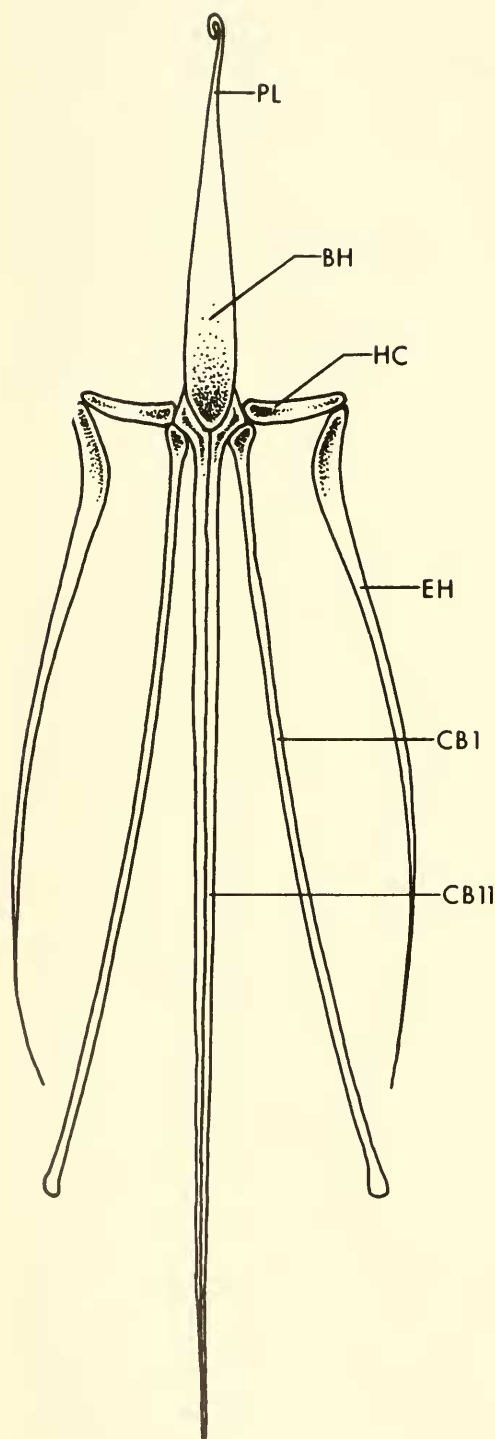


Fig. 8. Hyoid apparatus, ventral view: *Anolis carolinensis* (BYU 13768).

muthu 1937), *Chlamydosaurus* (Beddard 1905, DeVis 1883), *Phrynocephalus* (Haas 1973), *Physignathus* (Kesteven 1944), and *Uromastix* (Poglayen-Neuwall 1954, Versluys 1898, El Toubi 1947b, Tilak 1964b). In general, the agamid hyoids resemble closely those of the iguanids. In *Uromastix* the basihyoid is slender and laterally extended; the hyoid cornua are directed anterolaterally (Tilak 1964b). The short and widely separated second ceratobranchials extend posteriorly from the basihyoid. The first ceratobranchials extend posteriorly from the basihyoid. The first ceratobranchials articulate at the union of the hyoid cornua and the basihyoid. They comprise the longest elements of the hyoid. The epihyals attach to the distal ends of the hyoid cornua and have, at their distal ends, epibranchials that may attach to the distal end of the first ceratobranchials. In *Agama* (Fig. 9) the hyoid is similar except that the basihyoid is more massive and the second ceratobranchials are aligned more closely together. In *Calotes* and *Draco* the hyoids are elongated and narrow. The second ceratobranchials are exceptionally long and slender, lying close together at the midline, whereas

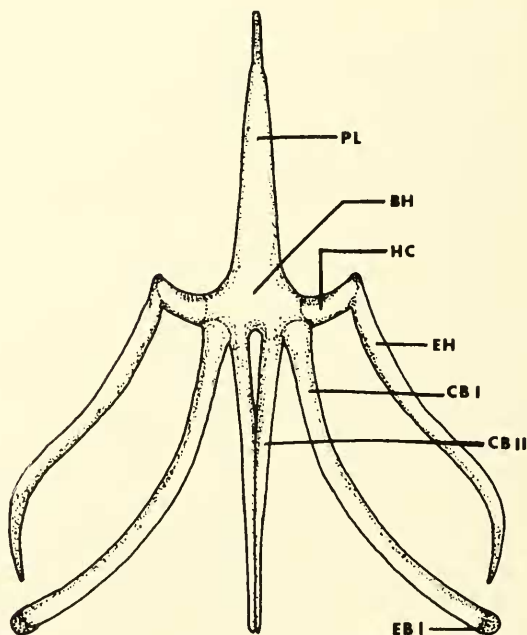


Fig. 9. Hyoid apparatus of *Agama agama* (BYU 18147), ventral view.

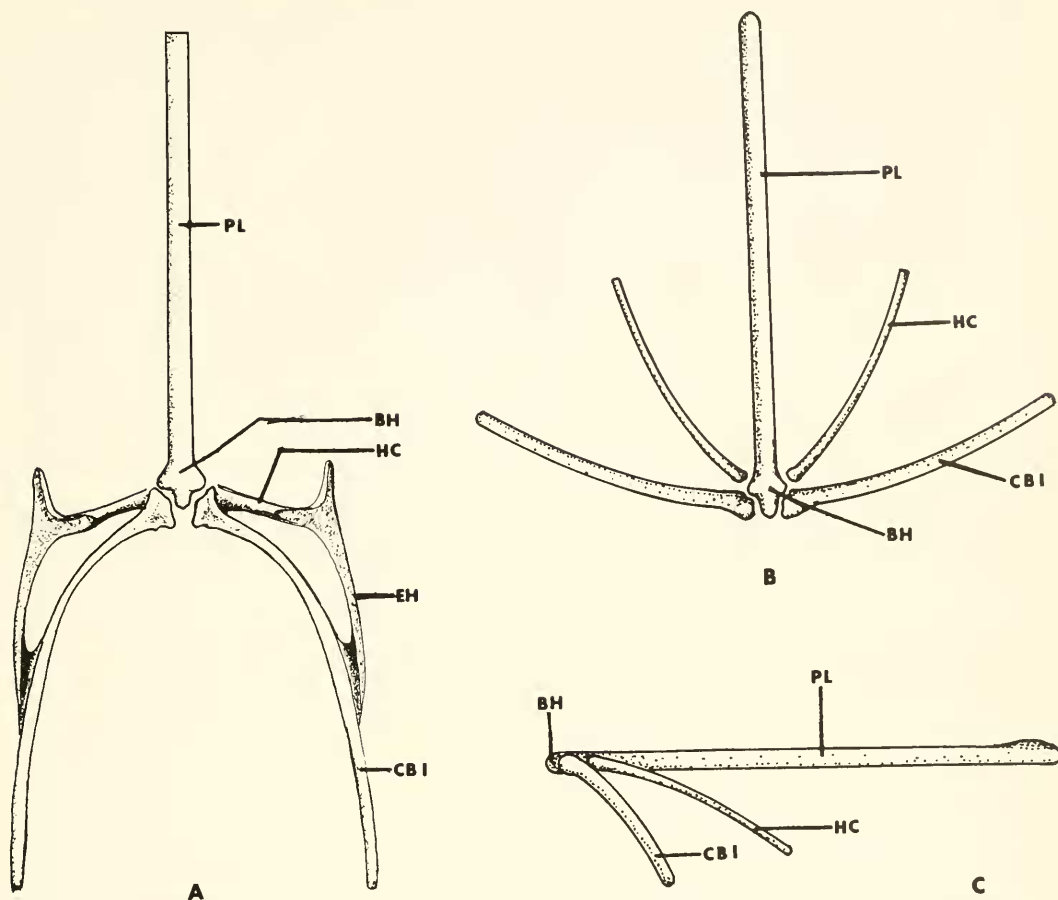


Fig. 10. Hyoid apparatus: A, *Chamaeleon namagyensis* (USNM 161275); B, *Chamaeleon brevicornis* (BYU 12422), ventral views; C, same as B, lateral view.

the epihyals are very short and not connected by epibranchials. In *Chlamydosaurus* the basihyoid is massive and bears two hornlike projections; these extend laterally to articulate with the hyoid cornua, which form short tapering tips on these projections. The second ceratobranchials appear to have been lost unless they are represented by two very small knobs on the posteromedial border of the basihyoid. The first ceratobranchials are extremely elongated, extending posterolaterally and composed of two pieces. The very long proximal piece articulates distally with the second piece, which is about one-fifth the length of the proximal. The epihyals are short or slender, and articulate at the point where the hyoid cornua and the lateral projections of the basihyoid attach. In *Physignathus* the hyoid exhibits a normal struc-

ture except that the first ceratobranchials are much longer than the second ceratobranchials.

In *Chamaeleo* the hyoid is distinctly different, with the basihyoid being little more than the basal part of the lingual process. The hyoid cornua extend anterolaterally about a third the length of the lingual process. The first ceratobranchials extend laterally and are short. The epihyals are small and attach to the hyoid cornua about half the distance from their distal ends. The second ceratobranchials are lost (Fig. 10-A, B, and C). Gnanamuthu (1937) described the hyoid apparatus for *Chamaeleo carcaratus* and reviewed previous studies of its function.

In the Scincidae the hyoids of *Scincus* (El Toubi 1938), *Eumeces* (Nash and Tanner 1970), Fig. 11, *Mabuya* (Richter 1933), and

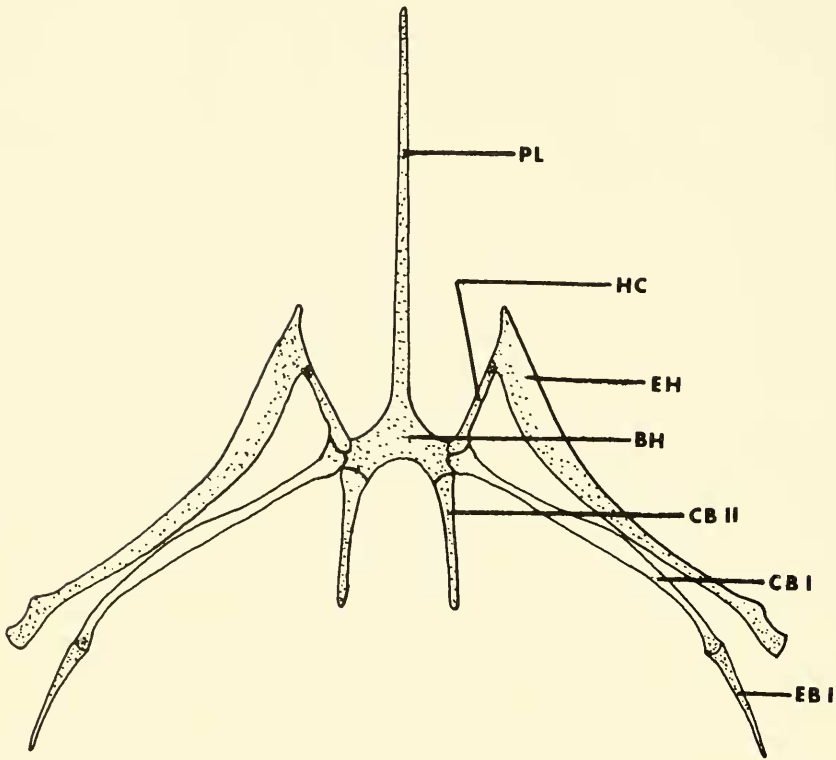


Fig. 11. Hyoid apparatus of *Eumeces gilberti* (BYU 31956), dorsal view. (After Nash and Tanner 1970)

Chalcides (Furbringer 1922, Richter 1933) have been described. All three arches are present and assume an unspecialized pattern. In all the basihyoid is broad rather than narrow, and the second ceratobranchials are very short and widely separated. The first ceratobranchials are elongate and slim. The hyoid cornua are short and slim, and articulate distally with the epihyals, which vary in form. They are simple rods in *Eumeces* and have enlarged proximal ends in the remaining genera. In *Scincus* the enlarged ends are simple and spoonshaped, but in *Chalcides* and *Mabuya* the shape is complex. In both genera the enlarged end has a short flange extending posterolaterally from the middle of the epihyal where the enlarged end terminates. These genera have a large hooklike second epibranchial associated with the distal end of the epihyal. It is attached in *Chalcides* and *Scincus* but separate in *Eumeces* and *Mabuya*. In all genera there is a short first epibranchial attached to the terminal end of the first ceratobranchial (Fig. 11).

Rieppel (1981) has examined the limbless scincoid genera *Acontias*, *Typhlosaurus*, and *Acontaphiops*. *Acontias* is described as being like *Anniella*, with the basihyal having a slender entoglossal process and being bifurcated posteriorly with its distinct posterolateral limbs articulating with first ceratobranchials. Hypohyal processes (hyoid cornua) are present in all species where they are T-shaped at their distal ends. In *Typhlosaurus* the hyoid is similar to *Acontias*, but the posterior first ceratobranchials are longer and hypohyals are absent. Rieppel calls attention to the fact that the hyoid of *Typhlosaurus* is identical to that of some Typhlopidae as described by List (1966) and Langebartel (1968). The hyoid of *Acontaphiops* is similar to that of *Typhlosaurus*.

In the teiid *Tupinambis*, the lingual process is detached from the basihyoid and embedded in the tongue. The second ceratobranchials are lost, and the epihyals and first ceratobranchials are connected by epibranchials.

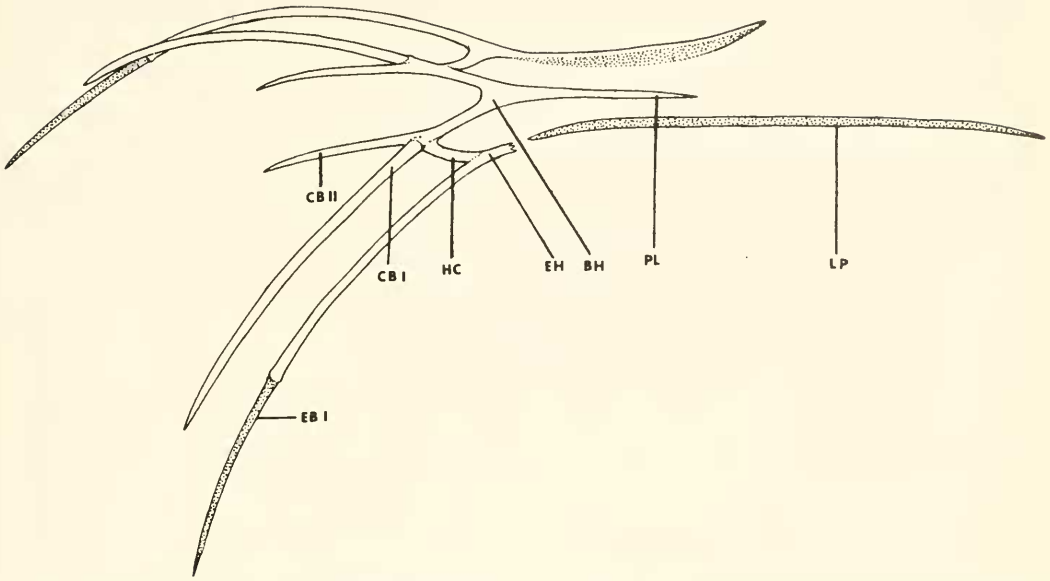


Fig. 12. Hyoid apparatus of *Cnemidophorus tigris* (BYU 31925). Dorsolateral view showing the detached lingual process (LP) and the extension of the body of the hyoid anteriorly as a spine.

The lingual process is also detached in *Cnemidophorus* (Fig. 12). The hyoid extends anteriorly as a short spine similar to that of iguanids except for its smaller size. It is embedded in connective tissue ventral to the lingual process and the tongue. The hyoid cornua extend anterolaterally from the basihyoid and articulate with the epihyals. The latter extend anteriorly, forming bladeliike cartilages that serve as lateral supports for the posterior half of the tongue and extend laterally to lie adjacent to the mandible. The posterior part of the epihyal extends posteriorly, curving laterally where it terminates as cartilage in loose connective tissue on the first ceratobranchial. Both ceratobranchials are present; the first extends posteriorly to terminate in the connective tissue with the cartilagenous first epibranchial. The epihyals and first ceratobranchials are not connected distally, although the ends are close together in a common connective tissue.

Ameiva lacks the second ceratobranchials. The first epibranchials are short, forming a knob on the end of the ceratobranchials.

In both *Ameiva* and *Cnemidophorus* the detached lingual process extends anteriorly to approximately the forking of the tongue. Posteriorly it is tightly enclosed in connective tissue between the elongate M. hypoglossus.

It terminates posteriorly, ventral to the laryngeal cartilages.

In *Anguis* (Anguidae) the hyoid is greatly reduced, with the second ceratobranchials and epihyals absent. The hyoid cornua are enlarged and extend anteriorly to parallel the lingual process for most of its length. In *Gerhronotus* and *Ophisaurus* the second ceratobranchials are also lost. The epihyals are present, however, and articulate with the distal ends of the hyoid cornua, which are more laterally directed than in *Anguis*.

In *Varanus* (Varanidae), the hyoid cornua is complex and is composed of two articulating cartilaginous rods, called by Sondhi (1958:159-160) the portio proximalis (hyoid cornu) and the portio distalis (epihyal):

Each has an anterior handlelike process and in life the two hooked ends cross each other beneath the tongue-sheath, with the handle of the portio proximalis lying dorsal to that of the portio distalis.

According to Sondhi (1958:159-160),

the proximal end of the portio proximalis fits into a roughly concave facet on the dorsolateral surface of the basihyoid, near the facet at which the posterior cornua articulates. From this point the portio proximalis extends obliquely upward, outward, and forward and at its termination curves inward to form the hook-shaped handle that is dorsoventrally flattened. The portio distalis is flattened at its proximal handlelike end, becomes rodlike as it passes backward and upward, and gradually

tapers at its distal end. It is disposed obliquely across the sides of the neck, its tapering end lying almost parallel to the proximal piece of the posterior cornua of its side.

Sondhi also indicates that the portio proximalis and portio distalis are attached to each other by a cartilaginous piece, with this attaching piece being folded at its outer margin like a cover of a folder so that one part of it becomes dorsal and the other ventral. The dorsal part is described as

narrower and is attached to the flattened, curved anterior end of the portio proximalis like the blades of scissors on its counterpart. The nature of attachment of the two pieces of the anterior cornua renders them capable of opening out to some extent like the covers of a folder.

The description of *V. monitor* (Sondhi 1958) and our dissection of *V. indicus* (BYU

40944) differ somewhat. We did not find a cartilaginous connection between the portio proximalis (hyoid cornu) and the portio distalis (epihyal). The only attachment is a lateral sheet of connective tissue that provides a loose connection. The expanded ends are not connected medially and are, therefore, folded as two separate sheets. Near the middle of the epihyal of *V. indicus*, a thin lateral expansion of cartilage is connected by a sheet of connective tissue to the lateral edge of the hyoid cornu. The distal end of the hyoid cornu is slightly flattened, but not expanded (Fig. 13).

The lingual process is shorter than that of *V. monitor* as figured by Sondhi, and does not extend anterior to the level of the expanded anterior ends of the hyoid cornu and the epihyal. In *Varanus* the first ceratobranchial and first epibranchial are greatly elongated, and the latter taper to a small rod terminating in connective tissue anterodorsal to the shoulder.

In *Heloderma* the second ceratobranchials are lost, and the epihyal is continuous with the hyoid cornu, forming a sigmoid curve. A joint exists at their point of articulation. The first ceratobranchials are also curved and diverge far laterally at their distal ends. In *Xenosaurus* as well, the second ceratobranchials are lost, but the epihyals are straight and long, with a hook at their distal end. The area of articulation between the epihyal and hyoid cornu is enlarged to form a knob. The hyoid cornua extend anterolaterally about two-thirds the length of the lingual process. McDowell and Bogert (1954) report that the hyoids of *Lanthanotus* and *Heloderma* are basically similar except *Lanthanotus* has lost the epihyals. Rieppel (1981) investigated *Lanthanotus* and found hypohyals (epihyal of McDowell and Bogert) that were reported absent by McDowell and Bogert (1954), although McDowell (1972:213) later did report them to be present. Rieppel rejects the argument of McDowell and Bogert that *Lanthanotus* is close to the origin of snakes. Rieppel (1981:435) states,

neither the shape of the basihyal nor any other feature of the hyobranchial skeleton of *Lanthanotus* shows a particular similarity to the ophidian hyoid.

Through the courtesy of Dr. Richard Zweifel we were privileged to examine the throat

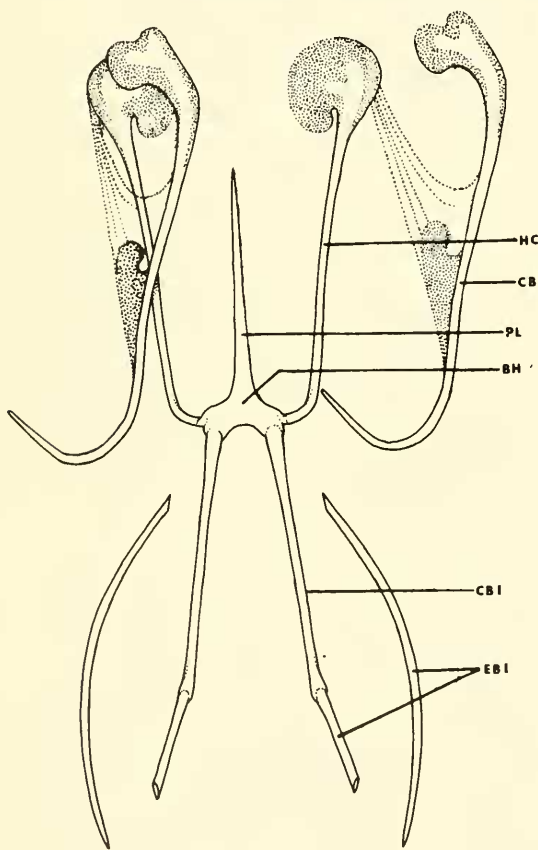


Fig. 13. Hyoid apparatus of *Varanus indicus* (BYU 40944). Ventral view with the left epihyal reflected to show the absence of a cartilage connection between it and the distal end of the hyoid cornu. Dotted lines extending from the cartilaginous median part of the epihyal represents connective tissue. The elongate first epibranchials are cut.

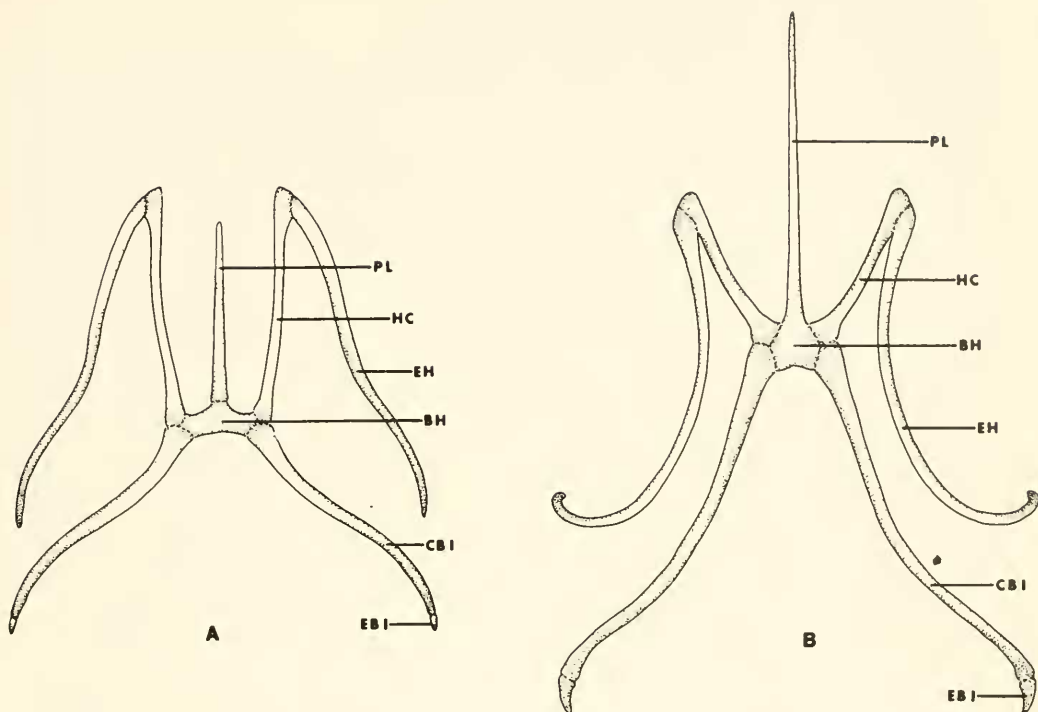


Fig. 14. Hyoid apparatus, ventral views: A, *Lanthanotus borneensis* (AMNH 87375); B, *Heloderma suspectum* (BYU 41436).

anatomy of *Lanthanotus borneensis* (AMNH 87375) and found the hyoid skeleton to be surprisingly similar to that of *Heloderma* (Fig. 14). Rieppel (1980, 1981) has, on the basis of cranial anatomy, concluded that *Lanthanotus* is intermediate in structure between *Heloderma* and *Varanus*. Branch (1982) arrived at a similar conclusion based on hemipeneal data. The hyoid of these genera have the same structures; however, in *Varanus* there has been considerable modification and specialization not found in the other genera.

In *Gerrhosaurus* (Cordylidae) the second ceratobranchials have been lost, but the first ceratobranchial and epihyal are retained. In *Zonurus* the second ceratobranchials are present but short. In *Xantusia* (Xantusiidae) the hyoid contains all the elements. The hyoid cornu extends dorsolaterally to articulate with the median edge of the expanded, flattened proximal end of the epihyal. From the flattened end the epihyal extends posterodorsally, tapering into a rod and terminating as a short epibranchial immediately posterior to the tympanum. The first ceratobranchial extends posterodorsally and curves

to terminate in the second epibranchial and in close association with the epibranchial of the epihyal.

The second ceratobranchial in *Xantusia* extends posterior with the distal end, curving laterad to form an open hook. It does not articulate with an epibranchial as in the epihyal and first ceratobranchial; however, a cartilaginous structure in close association with the distal end of the second ceratobranchial extends laterally and curves anteriorly to articulate with the basioccipital of the skull. Cope (1900) and Savage (1963) have referred to this structure as a free epibranchial. If this is an epibranchial, it is distinct and differs from all others in saurians we have seen. Its close association to the distal end of the second ceratobranchial (Fig. 15) is not articulated as in the other epibranchials and leads us to believe that the entire structure may represent fusions of other remnant gill bars. An examination of the entire structure (Fig. 15B) indicates to us that fusions have occurred. An articulation or close association of the distal ends of the epihyal and/or the second ceratobranchial occurs in many forms

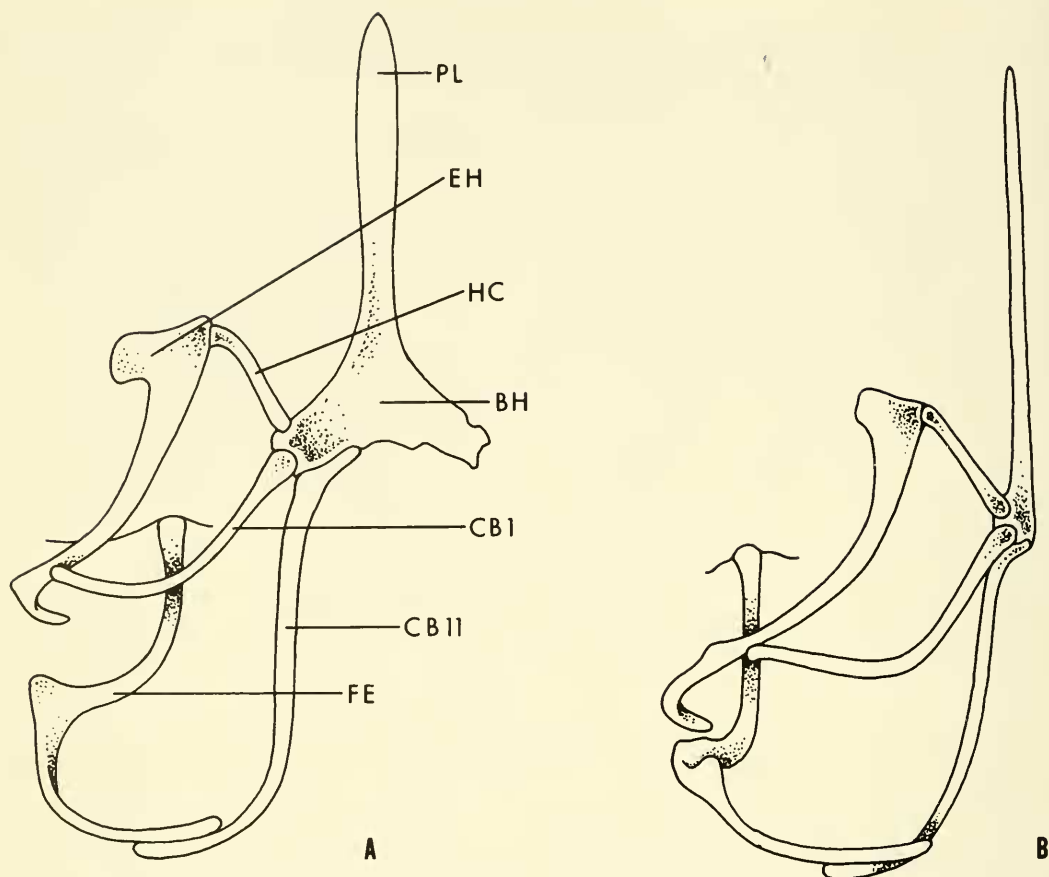


Fig. 15. Hyoid apparatus of *Xantusia vigilis* (BYU 21765): A, ventral view; B, lateral view. (FE = "free epibranchial")

but the "free epibranchial" is unique to the xantusids.

The hyoid of *Anniella* has been described by Cope (1892) and Rieppel (1981). According to Rieppel, the basihyal is bifurcated posteriorly and bears a long entoglossal process. It articulates posteriorly with first ceratobranchials, and small hyohyals (hyoid cornua) are present. These latter structures were considered absent by Cope and Langebartel (1968).

In *Amphisbaenia* all the elements are present, with the second ceratobranchials being short and widely separated. The hyoid cornu extends anterolaterally, with its distal end free. The epihyal articulates with the cornu about one quarter of its distance from the proximal end. The first ceratobranchial articulates at the point of articulation between the hyoid cornu and the body of the hyoid. Its terminal end bears an epibranchial. All

the posterior projections of the hyoid extend straight back and remain unattached at their distal ends (Fig. 16).

Ophidia

The hyoids of snakes have been extensively discussed by Langebartel (1968) and others as follows:

Anomalepididae

Anomalepis (Smith and Warner 1948), *Helminthophis* (List 1966, Langebartel 1968), *Liotyphlops* (List 1966, Langebartel 1968).

Typhlopidae

Typhlophis (Evans 1955, List 1966), *Typhlops* (List 1966, Langebartel 1968).

Leptotyphlopidae

Leptotyphlops (Smith and Warner 1948, List 1966, Langebartel 1968, Oldham, Smith, and Miller 1970).

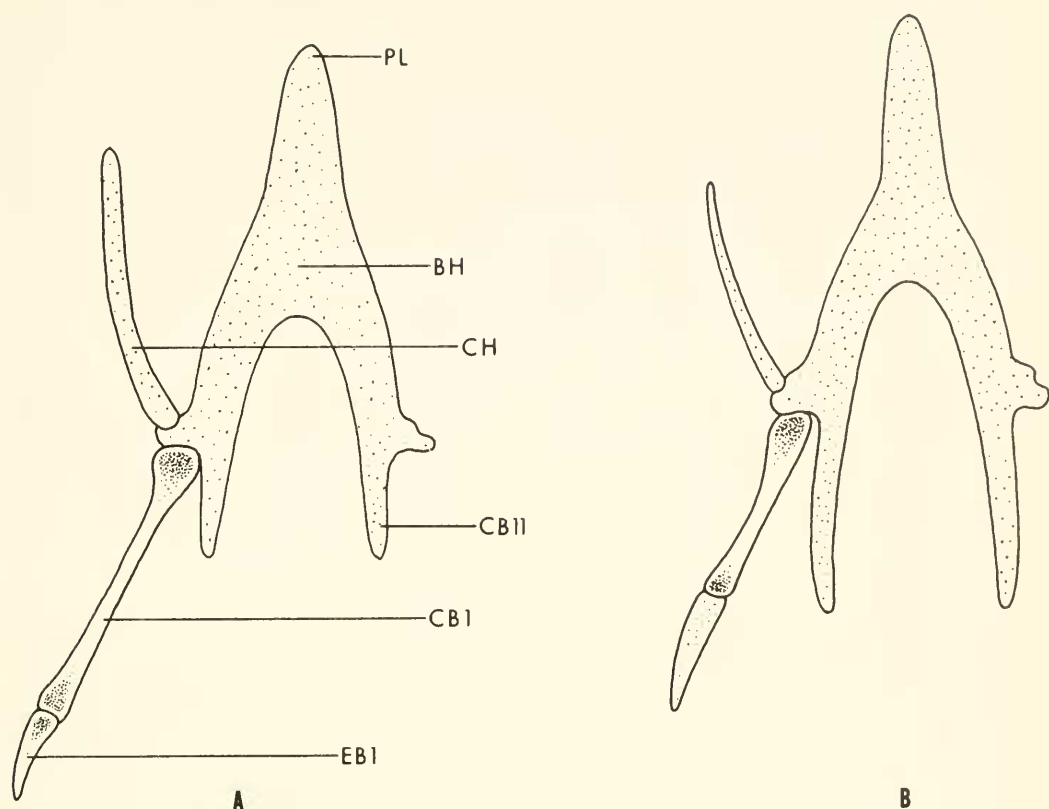


Fig. 16. Hyoid apparatus, ventral views: A, *Amphisbaenia cornura* (BYU 16127); B, *Amphisbaenia kingi* (BYU 16148).

Uropeltidae

Platyplacturus (Langebartel 1968), *Plectrurus* (Rieppel 1981), *Rhinophis* (Smith and Warner 1948, Langebartel 1968), *Silybura* (Langebartel 1968).

Aniliidae

Anilius (Smith and Warner 1948, Langebartel 1968, Rieppel 1981), *Cylindrophis* (Smith and Warner 1948, Langebartel 1968).

Xenopeltidae

Xenopeltis (Smith and Warner 1948, Langebartel 1968).

Boidae

Aspidites (Smith and Warner 1948, Langebartel 1968), *Boa* (Langebartel 1968), *Calabaria* (Langebartel 1968), *Charina* (Langebartel 1968), *Chondropython* (Langebartel 1968), *Constrictor* (Langebartel 1968), *Enygrus* (Langebartel 1968),

Epicrates (Langebartel 1968), *Liasis* (Langebartel 1968), *Lichanura* (Langebartel 1968), *Loxocemus* (Smith and Warner 1948, Langebartel 1968), *Nardoana* (Langebartel 1968), *Python* (Furbringer 1922, Langebartel 1968, Oldham, Smith, and Miller 1970), *Sanzinia* (Langebartel 1968), *Trachyboa* (Langebartel 1968).

Colubridae

Achalinus (Langebartel 1968), *Achrochordus* (Smith and Warner 1948, Langebartel 1968), *Adelphicus* (Langebartel 1968), *Amblycephalus* (Smith and Warner 1948, Langebartel 1968), *Aparallactus* (Langebartel 1968), *Apostolepis* (Langebartel 1968), *Atretium* (Langebartel 1968), *Boiga* (Langebartel 1968), *Carphophis* (Smith and Warner 1948, Langebartel 1968), *Cerberus* (Langebartel 1968), *Chersodromus* (Langebartel 1968), *Chersydrus* (Langebartel 1968), *Chrysopelea*

(Langebartel 1968), *Clelia* (Langebartel 1968), *Coluber* (Walter 1887, Langebartel 1968), *Coniophanes* (Langebartel 1968), *Conopsis* (Langebartel 1968), *Conopsis* (Langebartel 1968), *Crotaphopeltis* (Langebartel 1968), *Cyclagras* (Langebartel 1968), *Dasypeltis* (Smith and Warner 1948, Langebartel 1968), *Dendrophidion* (Langebartel 1968), *Diadophis* (Langebartel 1968), *Dipsadoboa* (Langebartel 1968), *Dispholidus* (Langebartel 1968), *Dromophis* (Langebartel 1968), *Drymarchon* (Langebartel 1968), *Drymobius* (Langebartel 1968), *Dryophis* (Langebartel 1968), *Elaphe* (Langebartel 1968), *Elapomorphus* (Langebartel 1968), *Elapops* (Langebartel 1968), *Enhydrus* (Langebartel 1968), *Enulius* (Langebartel 1968), *Farancia* (Langebartel 1968), *Ficimia* (Langebartel 1968), *Fimbrios* (Langebartel 1968), *Geophis* (Langebartel 1968), *Haldea* (Langebartel 1968), *Haplopeltura* (Langebartel 1968), *Heterodon* (Weaver, 1965, Langebartel 1968), *Homalopsis* (Langebartel 1968), *Lampropeltis* (Langebartel 1968), *Leptodeira* (Langebartel 1968), *Leptophis* (Langebartel 1968), *Manolepis* (Langebartel 1968), *Masticophis* (Langebartel 1968), *Mehelya* (Langebartel 1968), *Natrix* (Sondhi 1958), *Nerodia* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Ninia* (Langebartel 1968), *Nothopsis* (Langebartel 1968), *Ophedrys* (Langebartel 1968, Cundall 1974), *Oxybelis* (Langebartel 1968), *Oxyrhabdium* (Langebartel 1968), *Pituophis* (Smith and Warner 1948, Bullock and Tanner 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Psamaodynastes* (Langebartel 1968), *Rhadineae* (Langebartel 1968), *Rhadinella* (Langebartel 1968), *Rhinocheilus* (Langebartel 1968), *Salvadora* (Langebartel 1968), *Sibynomorphus* (Langebartel 1968), *Sibynophis* (Langebartel 1968), *Sonora* (Langebartel 1968), *Tantilla* (Langebartel 1968), *Thamnophis* (Bullock and Tanner 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Toluca* (Langebartel 1968), *Trimorphodon* (Langebartel 1968), *Tropidonotus* (Langebartel 1968), *Xenodermus* (Langebartel 1968), *Xenodon* (Weaver 1965).

Elapidae

Acanthophis (Langebartel 1968), *Aspidelaps* (Langebartel 1968), *Bungarus* (Langebartel 1968), *Calliophis* (Langebartel 1968), *Demansia* (Langebartel 1968), *Dendraspis* (Langebartel 1968), *Denisonia* (Langebartel 1968), *Doliophis* (Langebartel 1968), *Elaps* (Langebartel 1968), *Elapsoidea* (Langebartel 1968), *Furina* (Langebartel 1968), *Hemachatus* (Langebartel 1968), *Hemibungarus* (Langebartel 1968), *Leptomicrurus* (Langebartel 1968), *Maticora* (Langebartel 1968), *Micruroides* (Langebartel 1968), *Micrurus* (Smith and Warner 1968, Langebartel 1968), *Naja* (Langebartel 1968, Kamal, Hamouda, and Mokhtar 1970), *Notechis* (Langebartel 1968), *Ogmodon* (Langebartel 1968), *Pseudelaps* (Langebartel 1968), *Ultocalamus* (Langebartel 1968).

Eydorphidae

Aipysurus (Langebartel 1968), *Hydrophis* (Langebartel 1968), *Kerilia* (Langebartel 1968), *Lapemis* (Smith and Warner 1948, Langebartel 1968), *Laticauda* (Langebartel 1968), *Thalasophina* (Langebartel 1968).

Viperidae

Aspis (Langebartel 1968), *Atheris* (Langebartel 1968), *Atractaspis* (Langebartel 1968), *Bitis* (Langebartel 1968), *Causus* (Langebartel 1968), *Cerastes* (Langebartel 1968), *Echis* (Langebartel 1968), *Pseudocelestes* (Langebartel 1968), *Vipera* (Langebartel 1968, Furbringer 1922).

Crotalidae

Agkistrodon (Smith and Warner 1948, Langebartel 1968), *Bothrops* (Langebartel 1968), *Crotalus* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Lachesis* (Langebartel 1968), *Sistrurus* (Langebartel 1968), *Trimeresurus* (Langebartel 1968).

In snakes the hyoid apparatus is greatly reduced, with the hyoid cornua being lost and the remainder of the processes simplified. Essentially the snake hyoid consists of a body plus a lingual process and what is thought to be the second ceratobranchials, which are fused to the body of the hyoid (Figs. 17A and B, 29). The variations found in ophidian hyoids have been discussed by Furbringer

(1922), Versluys (1936), Gnanamuthu (1937), Smith and Warner (1948), Sondhi (1958), Albright and Nelson (1959), List (1966), Underwood (1967), Langebartel (1968), Rieppel (1981), and others. There are four major morphological types that can be distinguished in snakes. These correspond in shape roughly to the letters M, Y, and V, and to a parallel type 11. The most complete survey of the hyoids of snakes is presented by Langebartel (1968), and we have based much of our remarks on his study.

Hyoids possessing the M shape are found exclusively in the family Anomalepididae, which has only four genera, *Anomalepis*, *Liotyphlops*, *Helminthophis*, and *Typhlophis*. In this group the hyoid has a body and the second ceratobranchials. All other processes are lost, including the lingual process.

A Y-shaped hyoid is found in the Tylopidae and Leptotyphlopidae. The body of the hyoid possesses a lingual process and has hyoid cornua (second ceratobranchials) that project posteriorly. The possession of a lingual process is variable, with it being absent according to List (1966) in *Typhlops pusillus* and *T. lumbricalis*. In *T. reticulatus*, *T. platycephalus*, and *T. blandfordi lestradei* the hyoid cornua are separated from the body. *Leptotyphlops* has a normal Y type hyoid.

The V-shaped hyoid is found in the Aniliidae, Boidae, Uropeltidae, and Zenopeltidae. In this type of hyoid the lingual process is absent and the hyoid cornua may be attached or unattached. There is much intraspecific variation in the latter character. In some specimens of *Charina bottae* the cornua are attached, although they are unattached in others. Langebartel (1968) considers the curving arches to be the first ceratobranchials.

The 11 type hyoid is found in the colubrids, crotalids, elapids, hydrophids, viperids, and some genera of the boidae (*Casarea*, *Trachyboa*, and *Tropilophis*). The second ceratobranchials of this type are usually long, parallel rods attached to a slim hyoid body (Fig. 17). The resulting structure resembles a tuning fork in appearance. A few snakes have a hyoid body, triradiate in appearance and with a short lingual process. Such a structure is figured by Sondhi (1958) for *Natrix (Xenochrophis)*, in which:

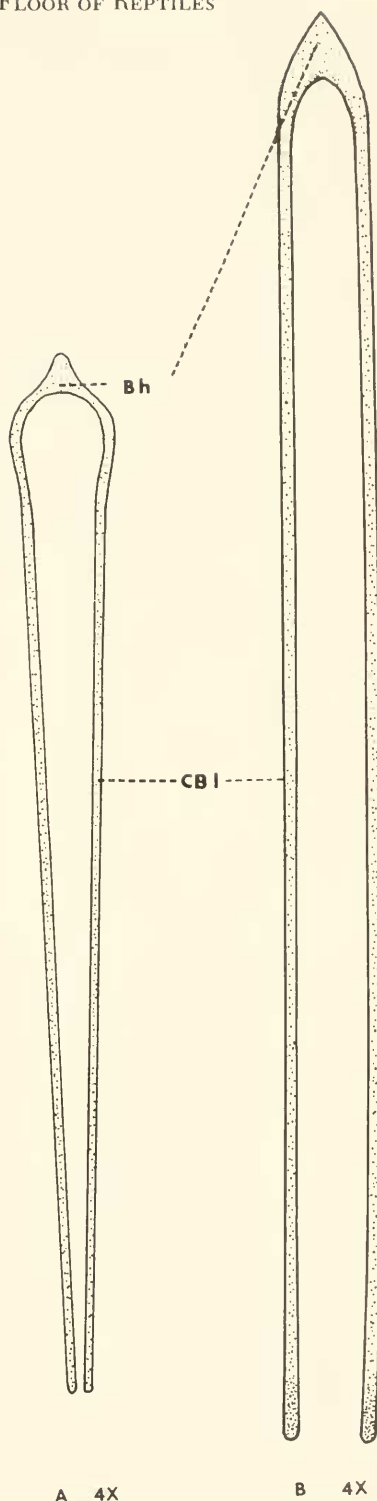


Fig. 17. Hyoid apparatus, ventral views: A, *Pituophis m. deserticola* (BYU 3072); B, *Crotalus viridis lutosus* (2089). Both are from adult individuals and drawn at 4X actual size.

the basihyoid lies ventral to the trachea and dorsal to the posterior terminations of the omohyoideus and sternohyoideus muscles.

The processes form elongated rods that lie ventral and extend posteriorly and parallel, with their terminal ends enclosed in the tips of the base of the tongue. In *Pituophis*, the basihyoid is ventral to the tongue at about the level of the angle of the jaws. The ceratobranchials extend and curve posterolaterally from the basihyoid for a short distance to a lateral position and then extend posteriorly, lateral to the tongue and parallel to each other, to the posterior tip of the tongue. In *Crotalus* the same obtains anteriorly with the basihyoid and the anterior part of the ceratobranchials; however, the posterior third of the latter converge ventrally to become closely associated along the ventromedian of the tongue and diverge slightly near their ends to become imbedded in muscle and connective tissue (Fig. 28, Romer 1950:fig. 421-C, Langebartel 1968:figs. 3, 4). For detailed description of the hyoid of individual genera of snakes, see Langebartel (1968).

III. MUSCLES OF THE BUCCAL FLOOR: GENERAL

The buccal floor is composed of several interwoven sheets of muscles. These sheets can be separated into two major groups: the hypobranchial musculature and the muscles of the associated branchial arches. The hypobranchial muscles are derived from the myotomes of the occipital and cervical somites, whereas the muscles of the branchial arches come from the visceral muscle plates formed in the branchial region. The tongue, for the most part, is also derived from the occipital somites. Because of the close associations of some of the somites with both cranial and spinal areas, some muscles are innervated by both spinal and cranial nerves.

For the sake of convenience, we have separated our discussion of the buccal musculature into two major divisions: (1) the muscles associated with the hyoid apparatus and (2) those associated with other structures. The tongue is sufficiently important to be segregated from these categories and is considered under a separate heading.

The nomenclature of muscles of reptiles has not been standardized; however, tables of synonyms can be found in Edgeworth (1935), Langebartel (1968), Haas (1973), and Schumacher (1973). Some of the more recent short summaries of the earlier papers on the myology of the buccal floor in reptiles can be found in Sondhi (1958), Langebartel (1968), Avery and Tanner (1971), Secoy (1971), and Varkey (1979). The remainder of this section is a brief account of the musculature of the buccal floor in selected reptiles as described by several earlier workers such as Edgeworth (1931), Graper (1932), Gnanamuthu (1937), Reese (1915 and 1932), Hacker and Schumacher (1955), Oelrich (1956), Sondhi (1958), Langebartel (1968), and others. It also should be noted that the more advanced reptiles have more complex muscular patterns when compared to primitive forms. This is seemingly true not only for orders, but also for family groups. A comparison of the advanced lizard *Varanus* and the primitive iguanids in the following sections serves as an illustration.

We refer to such forms as *Gavialis*, *Trionyx*, *Natrix* (*Xenochrophis*), *Varanus*, and other genera. These should be credited to Gnanamuthu (1937) or Sondhi (1958) if not otherwise noted.

The musculature of the following reptiles has been studied.

Chelonia

Pelomedusidae

Pelusios (Poglayen-Neuwall 1953a).

Chelidae

Batrochemys (Poglayen-Neuwall 1953a),

Chelodina (Poglayen-Neuwall 1953a).

Chelydridae

Chelydra (Camp 1923, Graper 1932, Poglayen-Neuwall 1953a, Schumacher 1973), *Kinosternon* (Poglayen-Neuwall 1953a, Schumacher 1973), *Sternotherus* (Poglayen-Neuwall 1953a, Schumacher 1973).

Testudinidae

Chrysemys (Poglayen-Neuwall 1953a, Ashley 1955, Schumacher 1973), *Cuora* (Poglayen-Neuwall 1953a), *Clemmys* (Graper 1932, Poglayen-Neuwall 1953a, Schumacher 1973), *Deirochelys* (Shah 1963), *Emys*

(Walter 1887, Schumacher 1973), *Gopherus* (George and Shad 1954), *Graptemys* (Poglayen-Neuwall 1953a), *Geochelone* (Bojanus 1819, Graper 1932, Lubosch 1933, Edgeworth 1935, Poglayen-Neuwall 1953a, George and Shad 1955, Schumacher 1973), *Malaclemys* (Poglayen-Neuwall 1953a), *Pseudemys* (Ashley 1955, Poglayen-Neuwall 1953a, Schumacher 1973), *Terrapene* (Poglayen-Neuwall 1953a).

Trionychidae

Lissemys (George and Shad 1954, Sondhi 1958, Schumacher 1973), *Trionyx* (Graper 1932, Lubosch 1933, Poglayen-Neuwall 1953a, Sondhi 1958, Schumacher 1973).

Cheloniidae

Caretta (Poglayen-Neuwall 1953a, Schumacher 1973).

Dermochelyidae

Dermochelys (Poglayen-Neuwall 1953a, 1953/54, Schumacher 1973).

Rhynchocephalia

Sphenodontidae

Sphenodon (Osawa 1898, Camp 1923, Byerly 1926, Lubosch 1933, Edgeworth 1935, Lightoller 1939, Kesteven 1944, Rieppel 1978).

Lacertilia

Gekkonidae

Coleonyx (Camp 1923), *Gekko* (Camp 1923, Lubosch 1933), *Gymnodactylus* (Brock 1938, Kesteven 1944), *Hemidactylus* (Zavattari 1908, Ping 1932, Edgeworth 1935, Gnanamuthu 1937), *Platyedactylus* (Sanders 1870, Poglayen-Neuwall 1954), *Stenodactylus* (Camp 1923, Edgeworth 1935), *Tarentola* (Gnanamuthu 1937, Poglayen-Neuwall 1954), *Thecodactylus* (Kesteven 1944).

Dibamidae

Dibamua (Gasc 1968).

Iguanidae

Amblyrhynchus (Avery and Tanner 1971), *Anolis* (Kesteven 1944), *Basiliscus* (Gnanamuthu 1937), *Brachylophus* (Camp 1923,

Avery and Tanner 1971), *Callisaurus* (Cox and Tanner 1977), *Chalarodon* (Avery and Tanner 1971), *Conolophus* (Cox and Tanner 1977), *Crotaphytus* (Davis 1934, Robison and Tanner 1968), *Ctenosaura* (Oelrich 1956, Avery and Tanner 1971), *Cyclura* (Avery and Tanner 1971), *Dipsosaurus* (Avery and Tanner 1971), *Enyaliosaurus* (Avery and Tanner 1971), *Holbrookia* (Cox and Tanner 1977), *Iguana* (Mivart 1867, Edgeworth 1935, Poglayen-Neuwall 1954, Avery and Tanner 1971, Oldham and Smith 1975), *Oplurus* (Avery and Tanner 1971), *Phrynosoma* (Sanders 1874, Camp 1923, Jenkins and Tanner 1968), *Sauromalus* (Avery and Tanner 1964, 1971), *Sceloporus* (Secoy 1971), *Tropidurus* (Zavattari 1908, Edgeworth 1935), *Uma* (Cox and Tanner 1977), *Urosaurus* (Fanghella, Avery and Tanner 1975), *Uta* (Fanghella, Avery and Tanner 1975).

Agamidae

Agama (DeVis 1883, Lubosch 1933, Edgeworth 1935, Poglayen-Neuwall 1954, Harris 1963), *Amphibolurus* (Poglayen-Neuwall 1954), *Calotes* (Camp 1923, Gnanamuthu 1937, Poglayen-Neuwall 1954), *Chlamydosaurus* (DeVis 1883), *Draco* (Gnanamuthu 1937), *Leiolepis* (Sanders 1872, Poglayen-Neuwall 1954), *Phrynocephalus* (Kesteven 1944), *Physignathus* (Kesteven 1944), *Sitana* (Gnanamuthu 1937), *Uromastix* (Furbringer 1922, Kubosch 1933, Edgeworth 1935, George 1948, Poglayen-Neuwall 1954, Throckmorton 1978).

Chamaeleonidae

Chamaeleo (Mivart 1870, Zavattari 1908, Camp 1923, Lubosch 1933, Edgeworth 1935, Gnanamuthu 1937, Kesteven 1944, Poglayen-Neuwall 1954).

Scincidae

Eumeces (Zavattari 1908, Edgeworth 1935, Nash and Tanner 1970), *Mabuya* (Gnanamuthu 1937), *Tiliqua* (Lightoller 1934, Kesteven 1944, Poglayen-Neuwall 1954), *Trachysaurus* (Poglayen-Neuwall 1954).

Cordylidae

Cordylus (Camp 1923, Edgeworth 1935), *Gerrhosaurus* (Camp 1923).

Lacertidae

Cabrita (Gnanamuthu 1937), *Lacerta* (Walter 1887, Camp 1923, Edgeworth 1935, Poglayen-Neuwall 1954).

Teiidae

Ameiva (Poglayen-Neuwall 1954, Fisher and Tanner 1970), *Cnemidophorus* (Poglayen-Neuwall 1954, Fisher and Tanner 1970), *Tupinambis* (Zavattari 1908, Camp 1923, Edgeworth 1935, Poglayen-Neuwall 1954).

Anguinidae

Gerrhonotus (Camp 1923, Poglayen-Neuwall 1954), *Ophiosaurus* (Poglayen-Neuwall 1954).

Xenosauridae

Shinosaurus (Haas 1960), *Xenosaurus* (Camp 1923, Haas 1960).

Helodermatidae

Heloderma (Camp 1923, Poglayen-Neuwall 1954).

Varanidae

Varanus (Bradley 1903, Camp 1923, Edgeworth 1935, Gnanamuthu 1937, Lightoller 1939, Kesteven 1944, Poglayen-Neuwall 1954, Sondhi 1958).

Anniellidae

Anniella (Camp 1923).

Amphisbaenidae

Amphisbaena (Smalian 1885, Camp 1923), *Anopsibaena* (Smalian 1885), *Bipes* (Smalian 1885, Renous 1977), *Blanus* (Smalian 1885), *Rhineura* (Camp 1923), *Trogonophis* (Smalian 1885).

Xantusidae

Xantusia (Camp 1923).

Ophidia

Anomalopididae

Anomalepis (Haas 1968), *Helminthophis* (Langebartel 1968), *Liotyphlops* (Langebartel 1968).

Typhlopidae

Typhlophis (Evans 1955), *Typhlops* (Langebartel 1968).

Leptotyphlopidae

Leptotyphlops (Langebartel 1968, Oldham, Smith, and Miller 1970).

Uropeltidae

Platylectrurus (Langebartel 1968), *Rhinophis* (Langebartel 1968), *Uropeltis* (Langebartel 1968).

Aniliidae

Anilius (Langebartel 1968), *Cylindrophis* (Lubosch 1933, Langebartel 1968).

Xenopeltidae

Xenopeltis (Langebartel 1968).

Boidae

Boa (Gibson 1966), *Calabaria* (Langebartel 1968), *Charina* (Langebartel 1968), *Constrictor* (Langebartel 1968), *Epicrates* (Langebartel 1968), *Eryx* (Langebartel 1968), *Eunectes* (Anthony and Serra 1950, Langebartel 1968), *Liasis* (Langebartel 1968), *Python* (Lubosch 1933, Edgeworth 1935, Kesteven 1944, Frazzetta 1966, Langebartel 1968, Oldham, Smith, and Miller 1970), *Sanzinia* (Langebartel 1968), *Trachyboa* (Langebartel 1968).

Colubridae

Achalinus (Langebartel 1968), *Achrochordus* (Langebartel 1968), *Amblycephalus* (Langebartel 1968), *Aparallactus* (Langebartel 1968), *Atridium* (Langebartel 1968), *Cerberus* (Langebartel 1968), *Chersydrus* (Langebartel 1968), *Coluber* (Walter 1887), *Dasypeltis* (Langebartel 1968), *Dryophis* (Lubosch 1933), *Elaphe* (Albright and Nelson 1959, Langebartel 1968), *Enhydrus* (Langebartel 1968), *Fimbrios* (Langebartel 1968), *Haplopeltura* (Langebartel 1968), *Heterodon* (Langebartel 1968), *Mehylia* (Langebartel 1968), *Natrix* (Sondhi 1958), *Nerodia* (Langebartel 1968, Oldham, Smith, and Miller 1970, Varkey 1979), *Nothopsis* (Langebartel 1968), *Ophiodrys* (Cundall 1974), *Pituophis* (Oldham, Smith, and Miller 1970), *Sibynomorphus* (Langebartel 1968), *Sibynophis* (Langebartel 1968), *Thamnophis* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Tropidonotus* (Lubosch 1933), *Xenodermus* (Langebartel 1968), *Xenodon* (Langebartel 1968).

Elapidae

Denisonia (Langebartel 1968), *Doliophis* (Langebartel 1968), *Naja* (Lubosch 1933, Langebartel 1968), *Notechis* (Langebartel 1968), *Pseudechis* (Kesteven 1944).

Hydrophidae

Aipysurus (Langebartel 1968), *Hydrophis* (Langebartel 1968), *Laticauda* (Langebartel 1968), *Pelamis* (Langebartel 1968).

Viperidae

Aspis (Langebartel 1968), *Atractaspis* (Langebartel 1968), *Causus* (Haas 1952, Langebartel 1968), *Cerastes* (Langebartel 1968), *Echis* (Langebartel 1968), *Vipera* (Edgeworth 1935, Langebartel 1968).

Crotalidae

Agkistrodon (Langebartel 1968, Kardong 1973), *Bothrops* (Langebartel 1968), *Crotalus* (Langebartel 1968, Oldham, Smith, and Miller 1970), *Lachesis* (Lubosch 1933, Langebartel 1968).

Crocodilia

Crocodylidae

Alligator (Reese 1915, Lubosch 1933, Edgeworth 1935, Chiasson 1962, Poggelayen-Neuwall 1953b), *Caiman* (Schumacher 1973), *Crocodylus* (Camp 1923, Edgeworth 1935, Kesteven 1944, Sondhi 1958, Poggelayen-Neuwall 1953b).

Gavialidae

Gavialis (Sondhi 1958).

IV. BUCCAL FLOOR MUSCLES ASSOCIATED WITH THE HYOID APPARATUS

1. *M. geniohyoideum* (genioglossus)

The *M. geniohyoideus* originates on the mandible and inserts on the hyoid apparatus. In *Lissemys* the *M. geniohyoideus* consists of two bundles arising from the mandible and inserting on the second ceratobranchial. Two distinct parts of this muscle arise from separate although continuous sites on the mandible in *Trionyx*. Each part inserts individually on the second ceratobranchial. According to Sondhi (1958) one of these, the portio dorsalis, arises from the ventral surface of the second ceratobranchial. The other, the

portio ventralis, lies ventral to the portio dorsalis and dorsal to the *M. mylohyoideus* posterior and constrictor colli; it inserts on the second ceratobranchial just posterior to the portio dorsalis.

In *Deirochelys* and *Chelodina* one part (*M. genioglossus*) arises from the anterior end of the inner border of the dentary and inserts on the basihyoid. Another portion (*M. geniohyoideus*) arises from the inner side of the mandibular symphysis and passes posteriorly to insert on the proximal end of the hyoid cornua. A similar condition exists in *Lissemys* and *Geochelone elegans* except that the median fibers also insert on the median raphe.

The *M. geniohyoideus* of *Alligator* is a slender muscle separated into two bundles. The medial bundle inserts onto the second ceratobranchial, whereas the lateral attaches to the *M. sternohyoideus*. The *M. geniohyoideus* of *Gavialis* lies obliquely in the posterior part of the buccal floor, where it originates posteriorly along the inner border of the mandible; it extends posteriorly and medially to become a tendon at its insertion near the middle of the ventrolateral border of the ceratobranchial. In *Crocodylus* the *M. geniohyoideus* inserts on the ventrolateral aspect of the proximal part of the second ceratobranchial.

In *Sphenodon* (Byerly 1926) and *Chamaeleo* (Gnanamuthu 1937) it is narrow, whereas in *Mabuia*, *Cabrita*, *Anolis* (Gnanamuthu 1937), *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, *Sauromalus* (Avery and Tanner 1971), *Hemidactylus*, *Coleonyx*, *Tarentola* (Figs. 4, 5), *Chlamydosaurus* (Beddard 1906), *Uromastix*, *Xenosaurus* (Haas 1960), *Cnemidophorus* (Fisher and Tanner 1970, Presch 1971), *Heloderma*, *Gerrhonotus* (Camp 1923), *Anniella* (Bellairs 1950), *Shinisaurus* (Haas 1960), and *Dibamus* (Girgis 1961, Gasc 1968) it forms a broad sheet arising from the posteromedial border of the mandible and passing posteriorly. There it is divided into three to six slips that may interdigitate with the *M. mylohyoideus* (Fig. 18 A, B, C, D). The superficial lateral slips overlie the medial one posteriorly and insert on the first ceratobranchial ventral to the medial muscle. A deep lateral slip originates on the mandible dorsal to the

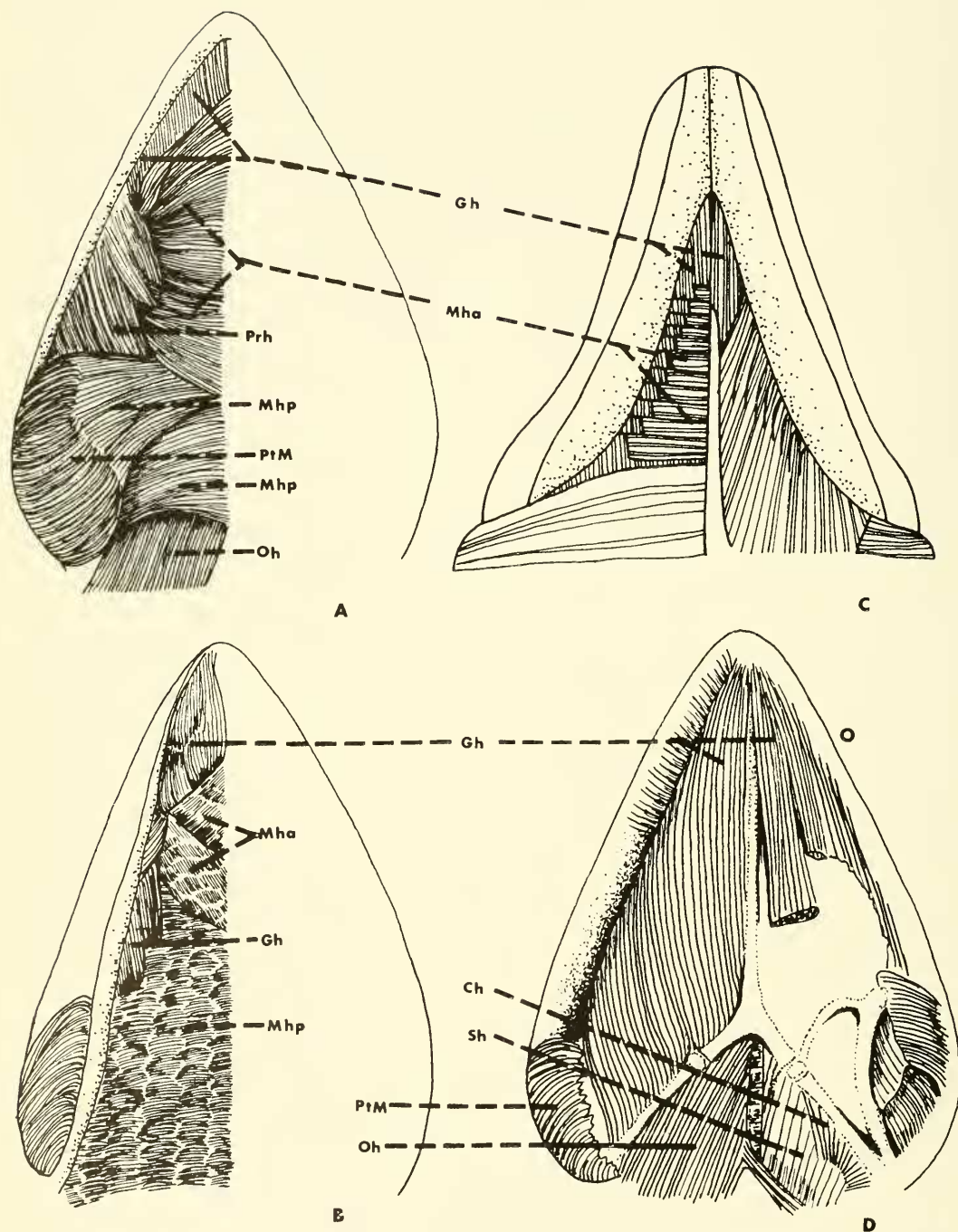


Fig. 18. Ventral view of the superficial supporting muscles of the throat and buccal floor: A, the gecko *Tarentola annularis* (BYU 18122); B, *Sceloporus magister* (BYU 30310); C, *Ameiva n. parva* (BYU 14396); and D, *Tarentola* with superficial muscles removed. The closely adhering skin in *Sceloporus* shows the scale impressions. Gh-Geniohyoideus; Mha-Mylohyoideus anterior; Prh-Prearticulo-hyoideus; Mhp-Mylohyoideus posterior; PtM-Pterygomandibularis; Oh-Omohyoideus.

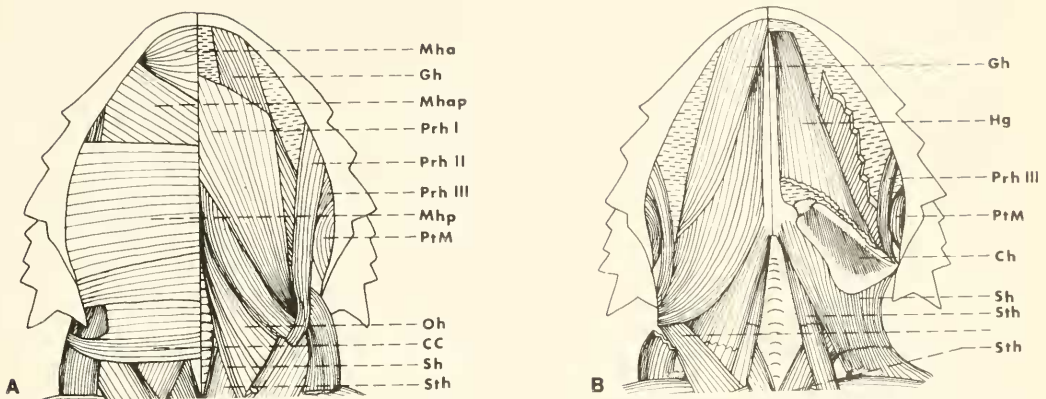


Fig. 19. Ventral view of *Phrynosoma platyrhinos*: A, Superficial myology; B, deeper muscles. (After Jenkins and Tanner 1968)

lateral superficial slip and inserts on the distal end of the epihyal.

The geniohyoideus in *Varanus* arises from the ventromedial border of the posterior part of the mandibular ramus and fans out posteriorly to cover the buccal floor and neck. The fibers converge posteriorly to insert on the ventromedial border of the proximal end of the second ceratobranchial and basihyoid, and the more median fibers insert in the fascia of the sternohyoideus and omohyoideus muscles. In the Iguanidae the medial fibers insert on the basihyoid or the anterior margin of the first ceratobranchials (Fig. 19), whereas in the gekkonids (*Tarentola* and *Coleonyx*) fibers are loosely divided into two bundles, the inner one inserting on the basihyoid and the other attached along the anterior margin of the first ceratobranchial (Fig. 18 D).

The M. geniohyoideus (genioglossus of Avery and Tanner 1971) of the iguane lizards consists of three parts, including the anterior fibers that arise on the ventromedial border of the mandible, where its fibers interdigitate with the M. intermandibularis anterior profundus and extend posteriorly (Fig. 18). There, the more medial fibers may insert on the lingual process, with the remainder passing ventral to the anterior cornu to insert on the first ceratobranchial (Fig. 19). A second division originates on the midventral raphe and inserts on the anterior border of the first ceratobranchial, with the third portion originating on the ventromedial border of the mandible, and interdigitates (as does the first part) before inserting on the lateral border of

the first ceratobranchial. A muscle deep to the lateral slip originates on the mandible and inserts on the posterior edge of the epihyal. This muscle may easily be included as a part of the lateral slip of the geniohyoideus. Jenkins and Tanner (1968), following Oelrich (1956), referred to it as the M. mandibulo-hyoideus III (Fig. 20). We have modified their designation to the M. mylohyoideus III, and wonder if the muscle is not a part of the M. geniohyoideus adapted to strengthen the lateral part of the mandibular-hyoid-buccal floor. We note that the same muscle is present in *Agama*, but less massive than in iguanids.

In the scincid *Eumeces* (Nash and Tanner 1970), the M. geniohyoideus originates from the anteromedial fifth of the mandible and inserts posteriorly by medial and lateral slips onto the hypoglossus, lingual fascia, and anterior margin of the first ceratobranchial. Some fibers also insert dorsally on the oral membrane and anteromedially on the cutaneous fascia.

Fisher and Tanner (1970) describe the M. geniohyoideus in *Ameiva* and *Cnemidophorus* (Teiidae) as originating on the medial surface of the dentary and inserting as five slips along the anterior margin of the body of the hyoid and the first ceratobranchial. Some dorsal fibers appear to insert on the ventral portion of the tongue. In these genera there is considerable interdigitation of the transverse and longitudinal muscles, as seen in Figure 18 C.

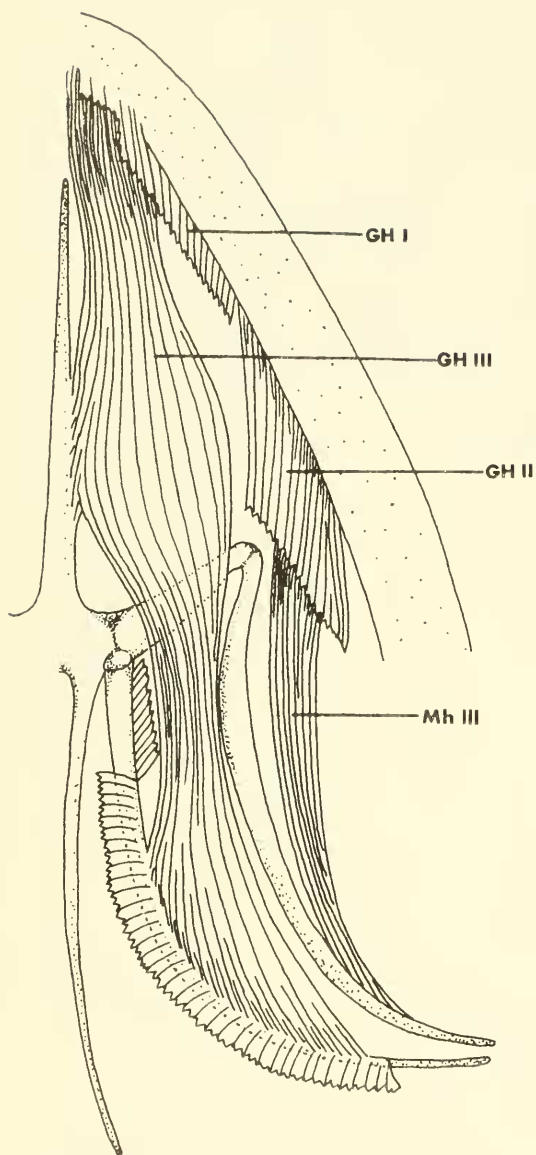


Fig. 20. Ventral view of the *M. geniohyoideus* of *Sauromalus* (BYU 32551) showing the origins (along mandible) and insertions (on hyoid apparatus). Gh-I-II-III divisions of the genioglossus and Mh III mandibulohyoideus.

In *Calotes*, *Sitana*, and *Chamaeleo* (Fig. 18) the median bundle is similar to that of the geckos, but there are two lateral bundles in *Calotes* and *Chamaeleo* and four in *Sitana*. In *Chamaeleo* the two lateral bundles are deeper and insert on the ceratobranchial. The most medial of these bundles also has an in-

sertion on the anterior cornu. In *Draco* there are four lateral bundles, but the median bundle is missing. One of the lateral bundles interweaves with the *M. mylohyoideus* anterior and another (*M. geniohyoideus* basibranchialis of Gnanamuthu 1937) is attached to the branchial process. The lateral bundles of the *M. geniohyoideus* of *Chamaeleo* and *Draco* produce the *M. adductor inferior labioris* of Gnanamuthu (1937) (Fig. 21).

In *Agama agama* the median fibers do not insert on the basihyoid, but extend ventral to it and insert on the first ceratobranchial. The anterior cornu and body of the hyoid are covered ventrally by the *M. geniohyoideus*. The deep lateral slip inserts on the epihyal and, except for its smaller size, is similar to that seen in the iguanids.

In snakes such as the anomalepidids, the *M. geniohyoideus* arises from the posterior half of the mandible and passes posteriorly as a broad sheet separated medially from its counterpart by the linea alba. It inserts on both the basihyal and the second ceratobranchial. In the anomalepidids a slender slip of muscle attaches to the tip of the dentary and the terminal part of the second ceratobranchial; it has been described by Langebartel (1968) as being either another portion of the *M. geniohyoideus* or the *M. ceratomandibularis*. In the anomalepidids there is some variation in this muscle. The origin is by a single head in the Leptotyphlopidae and in the genera *Rhinophis*, *Cylindrophis rufus*, *Sanzinia*, *Enhydria*, *Aidpysurus*, and *Bothrops*. There is more than one head of origin in the Typhlopidae and Uropeltidae.

Another portion of this complex (*M. geniohyoideus* of Langebartel 1968) is described as occurring only in the Anomalepididae, in which it originates from the posterior half of the lower jaw and inserts on the hyoid cornua and ceratobranchial. In *Natrix* (*Xenochrophis*) the *M. geniohyoideus* is covered ventrally by the *Mm. mylohyoideus* posterior and constrictor colli after arising from the ventromedial border of the mandible. The parallel fibers of the *M. geniohyoideus* insert on the lateral border of the basihyoid and the anterior border of the second ceratobranchial after passing obliquely to the midline. Varkey (1979) describes a second origin from the midventral raphe and fascia just anterior to

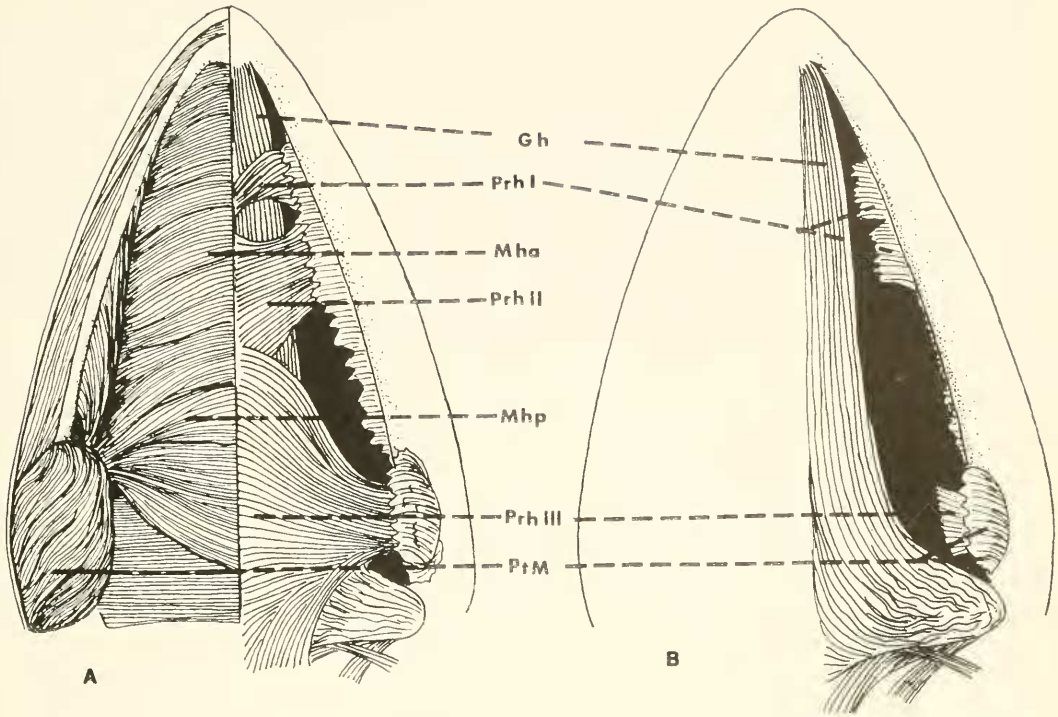


Fig. 21. Ventral view of *Chamaeleon brevicornis* (BYU 12422): A. superficial and muscles immediately dorsal to the superficial ones; B, geniohyoideus.

the lingual sheath. He considers the insertion to be the fascia of the hypoglossus muscle.

2. *M. genioceratoideus*

In *Varanus* the most lateral bundles of the *M. geniohyoideus* complex form a separate muscle (Sondhi 1958). It arises on the inner ventrolateral border of the mandible and extends posteriorly, where its fibers divide into two bundles. One bundle inserts on the lateral side of the handlelike position of the portio proximalis of the anterior cornu, with the second bundle inserting on the ventrolateral border of the middle cartilaginous part of the portio distalis of the second ceratobranchial. This muscle may exist in *Chamaeleo*, in which it has been described by Mivart (1870) as the ceratomandibular. A similar situation exists in *Chlamydosaurus* (Beddard 1950b, DeVis 1883).

3. *M. prearticulohyoideus*

The *M. prearticulohyoideus* is considered as a division of the *M. genioceratoideus* by Gnanamuthu (1937).

3a. *M. mandibulohyoideus*

In turtles, such as *Trionyx*, this muscle is large, lying in the ventrolateral region of the buccal floor and arising from the ventromedial border of the posterior part of the mandible; it inserts on the posterior region of the second ceratobranchial. In *Gavialis* the *M. prearticulohyoideus* is a thin muscle lying dorsal to the *M. ceratohyoideus* to insert on the posterior portion of the second ceratobranchial. Edgeworth (1935) has described a similar muscle in *Alligator*, which he calls the *M. branchiomandibularis*.

The second sheet (*M. mandibulohyoideus* I) is a long triangular muscle extending two-thirds the length of the mandible and lying lateral to the *M. mandibulohyoideus* II. This sheet originates along the ventromedial surface of the dentary and a small portion of the angular, with some fibers interdigitating with the more superficial musculature. The insertion is just posterolateral to that of the *M. mandibulohyoideus* II on the distal two-thirds of the posterior cornu.

The *M. mandibulohyoideus*, as described by Avery and Tanner (1971) for the iguanine lizards, by Robison and Tanner (1962) for *Crotaphytus*, and by Jenkins and Tanner (1968) for *Phrynosoma*, consists of two sheets. The most medial portion (*M. mandibulohyoideus* II) consists of a pair of small elongated bundles of fibers lying medial to the *M. mandibulohyoideus* I and inserting together on the midventral raphe of the throat. It originates as a narrow tendon from the mandibular symphysis. Each muscle inserts on the anterior border of the proximal end of the posterior cornu.

In *Varanus* Sondhi (1958) described it as a short muscle lying on the ventrolateral side of the neck, covering the posterior part of the mandible ventrally. It arises from the posterior and medial aspects of the mandible and extends almost straight back along the ventrolateral side of the neck to insert on the rodlike portion of the portio distalis of the anterior cornu.

4. *M. mandibuloproximalis*

The *mandibuloproximalis* has been described in *Varanus* by Sondhi (1958) as a slender muscle situated dorsal to the *M. geniohyoideus* and ventral to the *M. genioglossus*. It arises from the ventrolateral border of the ramus of the mandible, extending posteriorly and obliquely to pass dorsal to the handlelike portion of the portio distalis. Most of this muscle inserts on the outer margin of the handlelike portion of the portio proximalis, with some of its fibers becoming separated from the remainder and inserting on the lining of the buccal floor.

In the iguanid lizards the *M. mandibuloproximalis*, if present, forms a part of the *M. geniohyoideus* and cannot be distinguished from the latter muscle.

5. *M. ceratohyoideus*

The *M. ceratohyoideus* of *Sphenodon* is short and thin, having its origin on the second ceratobranchial and its insertion on the anterior cornu. Rieppel (1978) states that the presence of the *M. ceratohyoideus* lying between the ceratohyal and the first ceratobranchial and innervated by the *M. glossopharyngeus* is primitive. He further argues

that its failure to reach the lower jaw, as is the case in most lizards, is also perhaps an indication of its primitiveness.

In *Lissemys* the *M. ceratohyoideus* arises from the second ceratobranchial and inserts on the basihyoid. In *Trionyx* it arises from the distal half of the second ceratobranchial, enclosing this cartilaginous rod and extending anteromedially on the lateral side of the buccal floor to insert on the middle and anterior components of the basihyoid and on the knoblike anterior cornu.

In *Alligator* and *Crocodylus* it originates on the second ceratobranchial and inserts on the basihyoid. In *Gavialis* the *M. ceratohyoideus* lies dorsal to the basihyoid and is not visible in ventral view. The origin is on the dorsolateral border of the posterior cornu, with the muscle extending obliquely forward as a thin sheet on the ventral side of the buccal floor to insert on the dorsolateral side of the anterior cornu.

The insertion in *Sitana* is on the basihyoid. In *Varanus* it lies dorsal to the *M. geniohyoideus* on the ventrolateral side of the middle of the neck. The origin is from the ventrolateral border of the proximal piece of the second ceratobranchial, from which the muscle extends anteromedially to fan out over the ventrolateral side of the neck and insert on the handlelike portion of the portio distalis.

In the iguanid lizards this muscle has been described as the *M. branchiohyoideus* by Avery and Tanner' (1971). In *Ctenosaura* the muscle is ribbonlike and situated between the first ceratobranchial and second ceratobranchial of each side of the hyoid apparatus. The origin is along most of the anterior two-thirds of the first ceratobranchial, with the insertion on the posterior half of the second ceratobranchial. This pattern is duplicated in *Chalarodon*, *Oplurus*, *Crotaphytus*, and all the remaining iguanine lizards except *Sauromalus*. In the latter the insertion is very narrow, by a single tendon from the proximal rim of the anterior border of the posterior cornu.

In *Phrynosoma* this muscle covers nearly the entire area between the anterior and posterior cornua of the hyoid (Fig. 19 B). Its origin and insertion are similar to that described above for other iguanids. In *Chamaeleo* the *M. ceratohyoideus* is a small thick mass aris-

ing from the posterolateral border of the basihyoid to pass anterodorsally and insert on the epihyal.

In *Eumeces* (Scincidae) the muscle is a narrow strap similar to that in the iguanid *Sauromalus*.

In the teiids, *Cnemidophorus* and *Ameiva*, this muscle has a similar origin to that of the iguanids, but fills the entire area between the anterior and posterior cornua (Fisher and Tanner 1970).

6. *M. cornuhyoideus*

The *M. cornuhyoideus* was described in *Varanus* by Sondhi (1958) as being immediately posterior to the *M. ceratohyoideus*; it is ventrally concealed by the basal branch of the tongue and extends between the anterior and posterior cornua. It arises from the ventrolateral border of the proximal piece of the second ceratobranchial and proceeds forward to insert on the outer margin of the portio proximalis of the anterior cornu, anterior to the latter's articulation with the basihyoid. This muscle has not been described in any other reptile.

7. *M. interportialis*

Sondhi (1958) has reported that in *Varanus* this slender muscle lies dorsal to the *M. ceratohyoideus* and ventral to the portio proximalis. The origin is on the ventrolateral side of the anterior portion of the portio proximalis, from which the muscle extends obliquely anteriorly to insert on the medial border of the handlelike portion of the portio distalis. Gnanamuthu (1937) did not describe this muscle for *Varanus* and probably considered it to be part of the *M. ceratohyoideus*. It has not been described in other reptiles.

8. *M. hypoglossolateralis*

The *M. hypoglossolateralis* has been described by Sondhi (1958) as a delicate strip of muscle lying above the hypoglossum of the turtle *Trionyx*. Its origin is on the dorsal surface of that cartilaginous plate from which it extends to the lining of the buccal floor on which it inserts. This muscle is also present in

Gopherus agassizi, and we suspect its presence in association with the hypoglossal cartilage of other Chelonia.

9. *M. entoglossohypoglossalis*

The *M. entoglossohypoglossalis* is another muscle described by Sondhi (1958) for *Trionyx*. It arises from the ventrolateral border of the anterior part of the lingual process and inserts dorsolaterally on the posterior surface of the hypoglossum.

10. *M. omohyoideus*

In turtles such as *Lissemys* the *M. omohyoideus* is thick and long, and has an anterior division into dorsal and ventral bundles. The dorsal bundle inserts on the medioproximal part of the first ceratobranchial, and the ventral bundle inserts on the basihyoid along with the *M. sternohyoideus*. In *Trionyx* the *M. omohyoideus* originates on the anterior border of the scapula and extends forward on the ventral side of the neck to converge anteriorly to form two bundles, a larger medial and small lateral, which insert on the proximal part of the second ceratobranchial. In *Chelodina* the *M. omohyoideus* arises from the middle of the coracoid, but in *Deirochelys*, *Lissemys*, and *Geochelone* it originates on the ventral end of the coracoid. In all genera the fibers pass anteriorly to insert on the ceratobranchials.

In *Alligator* the *M. omohyoideus* is a long, narrow, thick muscle that originates from the upper border of the coracoid and passes forward to insert on the middle of the second ceratobranchial. In *Crocodylus* the origin is from the anterior border of the scapula and the insertion on the second ceratobranchial. *Gavialis*, as described by Sondhi (1958), has a moderately broad muscle arising from the anterior border of the coracoid. As it passes anteriorly, it divides into two parts, a portio dorsalis and a portio ventralis. The portio dorsalis extends obliquely anteromedially as a narrow strap that terminates in fragile slips that merge into the tendon of the *M. sternohyoideus*. The portio ventralis is broad, and its fibers parallel the trachea, finally inserting on the short anterior part of the second ceratobranchial.

The *M. omohyoideus* is a large muscle that usually arises on the pectoral girdle and inserts on the hyoid. In *Sphenodon* it is a large sheet, but in *Varanus* it is slender and partly covered by the *M. sternohyoideus* along its medial border. We summarize from Gnana-muthu (1937:24) as follows: In *Varanus* it arises on the anterior border of the scapula to pass obliquely forward and insert on the anterior part of the proximal end of the second ceratobranchial close to its articulation with the basihyoid. A similar situation exists in *Hemidactylus*. In *Cabrita*, *Mabuia*, and *Chamaeleo* the insertion of the *M. omohyoideus* is on the anterior border of the basihyoid. In *Calotes* it inserts not only on the basihyoid, but also on the sides of the proximal part of the first ceratobranchial. In *Anolis* and *Sitana* it inserts only on the first ceratobranchial, but in *Draco* there are three bundles, two of which insert on the first ceratobranchial and the third on the second ceratobranchial. In *Chlamydosaurus* it originates on the clavicle and sternum and inserts on the posterior one-third of the ceratobranchial.

In the iguanid lizards, such as *Ctenosaura*, the *M. omohyoideus* has medial and lateral origins. Medially the fibers originate on the lateral tip of the transverse process of the interclavicle, whereas the lateral fibers originate on the lateral half of the anterolateral surface of the clavicle and the anterior border of the suprascapula. As the two bundles extend anteriorly they become continuous and insert together along the posterior edge of the second ceratobranchial. In all the iguanine lizards and *Oplurus* the fibers of the medial and lateral bundles are impossible to separate. *Chalarodon* shows a slightly different configuration, with both bundles being separated for their entire length.

The *M. omohyoideus* in the teiids *Ameiva* and *Cnemidophorus* is a thick muscle originating on the anterior border of the scapula and then proceeding anteroventrally to insert on the proximal end of the basihyoid and along the second ceratobranchial. In *Dibamus* it is extremely long, originating on the scapula and inserting on the distal two-thirds of the ceratobranchial.

In snakes this muscle is very small and passes anteriorly from its origin on the lateral body muscles just posterior to the distal end

of the hyoid apparatus to insert on the posterior portion of the ceratobranchials. It has been found in the Anomalepididae *Cylindrophis*, *Rhinophis*, and *Eryx c. colubrinus*.

11. *M. sternohyoideus*

The *M. sternohyoideus* is a complex of muscles that arises from the sternum and inserts on the hyoid in most reptiles (Fig. 19).

In both *Lissemys* and *Trionyx* the *M. sternohyoideus* is large and lies adjacent to the *M. omohyoideus*. It originates from the clavicle and passes anteriorly and medially to insert on the proximal part of the second ceratobranchial and the middle of the basihyoid. In *Crocodylus* the *M. sternohyoideus* has long tendons by which it inserts on the second ceratobranchials. In *Alligator* it is flat and broad, and originates from the ventral surface of the episternum and forms a short tendon that inserts on the *M. geniohyoideus*. In *Gavialis* the *M. sternohyoideus* is a broad flat muscle with an origin on the ventral anterior half of the episternum; it passes along the ventral side of the neck to meet its opposite member at the midline where it obscures the trachea ventrally (Sondhi 1958). As it approaches the hyoid apparatus it divides into two parts, with the outer part (portio externa) a broad band forming a large tendon that inserts on the inner border of the mandible. The inner bundle (portio interna) parallels the trachea to insert on the outer part of the posterior border of the basihyoid.

In *Sphenodon* it is flat, whereas in some lizards it becomes cordlike and inserts (Rieppel 1978) on the caudodorsal edge and dorsal surface of the first ceratobranchial, deep to and lateral to the insertion of the *omohyoideus*. In *Mabuia*, the *M. sternohyoideus* inserts on the basihyoid, whereas in *Anolis*, with its small basihyoid, the insertion is on the first ceratobranchial. In *Varanus* the *M. sternohyoideus* lies dorsal to the *M. constrictor colli* and ventral to the basihyoid and the proximal piece of the second ceratobranchial. It arises from the ventrolateral border of the clavicle and extends obliquely anteriorly to the ventral side of the neck, where it parallels the *M. omohyoideus* and inserts on the ventral side of the basihyoid and posterior portion of the lingual process. *Chamaeleo*

has a small lateral bundle of fibers that insert on the fascia of the lateral M. geniohyoideus.

The M. sternohyoideus of the iguanine lizards (Avery and Tanner 1971), is an extensive muscle sheet occupying a large area posterior to the anterior cornu and anterior to the sternum and clavicle. It originates from several heads on the clavicle, and its oblique fibers extend anteriorly to insert on the posterior surface of the anterior cornu. In all the iguanines and in *Chalarodon* the muscle appears broad and sheetlike. In *Oplurus*, it is narrow and cordlike.

In *Phrynosoma* the M. sternohyoideus is separated into three distinct muscles (Fig. 19). As described by Jenkins and Tanner (1968), the M. sternohyoideus I originates from the medial surface of the scapula and the most anterior part of the clavicle and inserts on the distal two-thirds of the anterior cornu. This muscle may be the M. sternothyroideus of other workers. The M. sternohyoideus II originates from the anterolateral surface of the sternum and inserts onto the posterodorsal surface of the basihyoid.

The M. sternohyoideus III is separate for its entire length, with an origin from the ventral surface of the anterior third of the sternum and an insertion on the dorsal surface of the most enlarged area of the posterior cornu.

In the agamid *Chlamydosaurus*, the M. sternohyoideus has a large origin from the sternum immediately deep to that of the M. omohyoideus. It expands and thins as it extends anteriorly to insert on the inner side of the ceratobranchial ventral to the M. omohyoideus. In *Uromastix* the origin is from both the sternum and the coracoid.

Nash and Tanner (1970) describe a superficial and a deep layer of this muscle in the skink *Eumeces*. The larger ventral or superficial layer originates from the posterior and ventral surfaces of the ceratobranchial I and medial to the corpus and inserts on the interclavicle with the M. sternocleidomastoideus, trapezius, and depressor mandibularis, and with the constrictor colli on the posterior and ventral surfaces of the anterior cornu. The dorsal or deep layer originates on the interclavicle and inserts on the posterior border of both anterior and posterior cornua.

In *Dibamus*, the M. sternohyoideus is a large strap originating from the sternum and coracoid and inserting on the distal tip of the ceratobranchial (Gasc 1968).

In the teiids *Ameiva* and *Cnemidophorus*, the M. sternohyoideus is broad, with an origin on the sternum and insertions on both the posterior and anterior cornua and the basihyoid.

In snakes the M. sternohyoideus is found as a separate muscle only in the Typhlopidae and Leptotyphlopidae. Its origin here is deep to the muscles on the linea alba. The fibers pass anteriorly to insert on the hyoid, usually on the entire posterior edge of each cornu.

12. M. sternothyroideus

In the turtle *Trionyx* the origin of the M. sternothyroideus is on the anterior border of the sternum. The muscles extend anteriorly to insert on the ventrolateral border of the posterior part of the basihyoid.

In lizards, the M. sternothyroideus normally has an origin on the anteromedial portion of the sternum, from which it extends anteriorly to insert along the length of the second ceratobranchials. This situation exists in *Hemidactylus*, *Mabuia*, *Cabrita*, *Anolis*, *Calotes*, and the iguanine lizards. In *Chamaeleo* the M. sternothyroideus extends laterally to insert on the distal end of the ceratobranchial. In *Varanus* the M. sternothyroideus lies dorsal to the Mm. omohyoideus and sternohyoideus. It originates as a thin sheet from the anteromedial half of the sternum and inserts on the anterior half of the proximal piece of the second ceratobranchial.

In the iguanine lizards the most medial series of fibers of the M. sternohyoideus complex, the M. sternothyroideus, may be separated from the other members of this group by their different origins and insertions. The origin consists of a small area of both the interclavicle and sternum. These fibers pass anteriorly and parallel to the trachea to insert on the basihyoid. Along its length this muscle is difficult to separate from the more lateral M. sternohyoideus, except in *Oplurus* and *Chalarodon*, in which both muscles are free and separated along their entire length.

The *M. sternothyroideus* of *Phrynosoma* was previously described by Jenkins and Tanner (1968) as the *M. sternohyoideus* 1.

13. *M. costocutaneous superior*

Because the shoulder girdle of snakes has been lost, the *M. omohyoideus*, *sternohyoideus*, and *sternothyroideus* cannot be identified. Therefore these muscles will be discussed here under the name *M. costocutaneous superior*.

In some snakes it is possible tentatively to identify the homologs of these three muscles. For example, in the *Typhlopidae* and the *Leptotyphlopidae*, the *M. sternohyoideus* is a distinct mass of fibers that arise from the ventral scales and adjacent rows of lateral scales and the ribs, extending anteriorly to the hyoid and surrounding muscles. In *Typhlops*, *Leptotyphlops*, *Rhinophis*, *Cylindrophis*, and *Achrochordus*, the anteriormost fibers of the complex extend to originate on the mandible and overlay the hyoid while having no connection with it. In *Cylindrophis* the fibers originate on the posterior or medial edge of the *M. constrictor colli*. In the anomalepidid snakes the insertion is on the posteromedial border of the basihyoid and second ceratobranchial. The insertion also extends to the base of the lingual process in most specimens. In *Agkistrodon*, *Bothrops*, and *Crotalus*, the insertion is most extensive on the median raphe and lingual process.

Sondhi (1958) describes three specific muscles present in *Natrix* (*Xenochrophis*) that are probably homologous to the *Mm. omohyoideus*, *sternohyoideus*, and *sternothyroideus*. The omohyoid portion arises from the skin on the ventrolateral part of the neck and then extends obliquely anteriorly to insert on the ventrolateral aspect of the basihyoid. In *Atridium*, this muscle has a cutaneous origin and inserts on the second ceratobranchial. The second muscle, absent in *Atridium* but possibly the *M. sternohyoideus*, originates from the skin in the ventrolateral region of the neck posterior to the *M. omohyoideus* and passes anteriorly to close proximity with the latter to insert on the outer border of the basihyoid. The sternothyroid part of this complex lies in the midline of the

neck over the ventral surface of the basihyoid, with its origin on the midventral portion of the cervical skin. The muscle inserts on the medial border of the basihyoid. In *Atridium* the sternothyroid portion of the complex has its origin from the second ceratobranchial, with some fibers intertwining with their opposite member at the midline.

14. *M. neurocostomandibularis*

According to Langebartel (1968), the *M. neurocostomandibularis* is present in all snakes except the *Anomalepididae*. In most snakes it is a broad sheet forming part of the *M. neurocostomandibularis* complex, but in some it is separate and narrow. It covers a large area of the head and in some is partially overlain by the *Mm. constrictor colli* and *costocutaneous superior*. Its origin is on the dentary, from which it proceeds posteriorly to insert variously on the hyoid apparatus.

The muscles of *Python sebae* (Frazzetta 1966) and *Boa constrictor* (Gibson 1966) that are innervated by the hypoglossal nerves form a single muscular complex, the *M. neurocostomandibularis*, and correspond roughly to the *M. geniohyoideus* of other reptiles. The complex extends between the mandibles and the second ceratobranchials. In both *Boa* and *Python* the origin is on the lower jaw and the insertion on the posterior part of the second ceratobranchial.

In *Natrix* (*Xenochrophis*), Sondhi (1958) describes the *M. neurocostomandibularis* as probably the *M. geniolateralis* because the latter muscle receives a branch from the hypoglossal nerve. Langebartel (1968) considered this muscle to be the *M. ceratomandibularis* as designated by Richter (1933). The proper identity of this muscle in the typhlopids, leptotyphloids, and anomalepidids is unknown to us. According to Langebartel (1968), the *M. ceratomandibularis* in snakes arises from the dentary and inserts on the anterior part of the hyoid and the tendinous inscription in the *M. neurocostomandibularis*.

Varkey (1979) describes the *M. neurocostomandibularis* as being very complex and having three separate heads in *Nerodia*. It is a wide flat muscle sheathing the neck and most of the lower jaw. One origin (the vertebral head) is on the aponeurosis of the dorsal

midline neck region. It passes under the constrictor colli to insert on the midline raphe. The costal head originates by narrow slips from the first seven anterior ribs and inserts on the midline raphe with the previous slips. The third or hyoid head has a double origin from the midventral raphe just median to the hyoid cornua. This branch is called *M. transversalis branchialis* by Langebartel (1968). It inserts on the origin of the other heads on the midline raphe.

15. *M. transversalis branchialis*

The *M. transversalis branchialis* appears variably and erratically in the families of snakes with the exception of the Anomalepididae, Typhlopidae, and Leptotyphlopidae, in which it is universally absent.

When present, this muscle arises from somewhere on the second ceratobranchial. In *Rhinophis*, the origin is on the medial edge, whereas in *Cylindrophis* it originates on the anterior two-thirds. In *Anilius* the entire length of the cartilage is involved.

The insertion of this muscle is usually on the median raphe, although in some snakes it is inserted on the fascia covering the *M. costocutaneous superior*.

In *Nerodia*, Varkey (1979) describes the *M. transversus branchialis* as originating on the midline raphe just anterior to *M. intermandibularis*'s anterior. It passes anterolaterally to insert broadly on the mucosa of the angulo-splenic articulation and narrowly on the lateral sublingual gland. Varkey indicates his usage of this muscle name is as in Albright and Nelson (1959), Cowan and Hick (1951), and Weaver (1965). Langebartel (1968) calls this muscle the dilator of the sublingual gland, using the name *M. transversalis branchialis* for a branch of what Varkey calls the *M. neurocostomandibularis*.

16. *M. hyotrachealis*

In most snakes the *M. hyotrachealis* arises from the second ceratobranchial, but in *Liotyphiops* and the leptotyphiopids the fibers are tied by connective tissue on the ventrolateral surface of the lining of the buccal floor. In the typhlopids the fibers originate in connective tissue on the hypaxial trunk muscles. In other snakes the *M. hyotrachealis*

originates on the lateral edge of the second ceratobranchial. In *Rhinophis* the origin is at the anterior quarter of the medial edge, while in *Cylindrophis maculatus* and *C. rufus* the origin is from the lateral edge about half-way down the ceratobranchial. In the boids it originates on the posterior half of the cartilage. In *Tropidophis* the origin is deep from the raphe of the *M. neurocostomandibularis*. In colubrids, viperids, and elaphids the origin varies extensively. In *Heterodon* and *Pseudaspis* the origin varies extensively. In *Heterodon* and *Pseudaspis* the origin is from the rib cage, while in *Agkistrodon* it may be either the rib cage or hyoid, indicating a split origin. In *Vipera aspis*, Edgeworth (1935) describes one head of the *M. hyotrachealis* as lying dorsal to the rib cage while the lateral head attaches to the hyoid. In *Cerastes* the single head originates from the ventral lining of the buccal floor.

The insertion of the *M. hypotrachealis* is normally from the trachea of the laryngeal-tracheal area, dorsal and anterior to the insertion of the *M. geniotrachealis*. In some genera (*Typhlops*, *Amblycephalus*, *Xenopeltis*, and *Agkistrodon piscivorus*) the insertion is on the ventral portion of the *M. geniolateralis*. In *Boa cookii*, *Notechis*, and others the *M. hypotrachealis* has a split insertion with attachments on dorsal and ventral sides of the geniotrachealis.

Varkey (1979) describes *Nerodia*'s hyotrachealis as thin and narrow and of a double origin. One head is just anterior to a transverse tendinous inscription of the *M. neurocostomandibularis*. The second or median head is from the lateral edge of the hyoid cornua. The heads join and insert on the larynx and trachea anterior to the insertion of the geniotrachealis.

V. BUCCAL FLOOR MUSCLES NOT ASSOCIATED WITH THE HYOID APPARATUS

The homologies of a number of the reptilian throat muscles not connected with the hyoid are unclear. We will present the most widely used terminology and present synonyms only when two or more names have had wide usage for the same muscle. Although the following muscles are not directly attached to the hyoid apparatus, they have a

close functional relationship and are therefore included (Figs. 18, 19, 20).

1. *M. constrictor superficialis*

The *M. constrictor superficialis* is found in *Trionyx* as a superficial muscular sheet lying ventral to the anterior region of the neck. It arises as a narrow slip from the skin covering the side of the neck and broadens to insert on the gular septum. In *Gavialis* it originates on the skin overlaying the angle of the jaw, surrounds the neck, and extends obliquely to insert on the gular septum.

In other reptiles, such as iguanid lizards, this muscle is probably homologous to much of the *Mm. constrictor colli* and intermandibularis posterior of Avery and Tanner (1971).

2. *M. constrictor colli*

The *M. constrictor colli* is an extensive superficial muscular sheet, originating on the middorsal aponeurosis of the neck and extending ventrad to insert on the posterior part of the midventral raphe or gular septum. In *Sphenodon* it forms a broad, thin, superficial sheet that completely encases the neck (Rieppel 1978, Fig. 1). It ensheathes the entire neck in *Chelodina* and *Deirochelys*, but in *Lissemys* the neck is only partly covered. The muscle arises from the dorsal fascia and inserts on the median raphe. It is continuous anteriorly with the *M. intermandibularis*. Sondhi (1958) lists this muscle as present in *Trionyx* and *Gavialis*, and Gnanamuthu (1937) recognized it in *Crocodylus* and *Trionyx*. In the Testudines and Crocodylia the *M. constrictor colli* is not attached to the hyoid, but has an insertion on the gular septum.

This muscle covers most of the lateral surface of the neck in *Amblyrhynchus*, *Chalarodon*, *Cyclura*, *Iguana*, and *Sauromalus*. It is much less extensive in *Brachylophus*, *Conolophus*, *Ctenosaura*, *Dipsosaurus*, *Oplurus*, *Crotaphytus*, and *Phrynosoma*.

In *Chamaeleo* the *M. mylohyoideus* posterior of Mivart (1870) corresponds to the *M. constrictor colli*. It originates on the occipital crest and inserts on the median raphe.

In the skink *Eumeces* the *M. constrictor colli* is a very broad sheet originating from the middorsal tympanic fascial and inserting on the median raphe. It covers most of the neck from the angle of the jaw to the interclavicle.

In the teiids *Cnemidophorus* and *Ameiva*, the muscle is as in *Eumeces*, but the anterior border interdigitates with the posterior border of the *M. cervicomandibularis*. Gnanamuthu (1937) figures this muscle to be in *Hemidactylus*, *Mabuia*, *Cabrita*, *Anolis*, *Calotes*, and *Draco*.

In snakes the *M. constrictor colli* appears erratically and is not constant in form within a single genus as indicated by *Python*. The muscle is normally broad and envelops the angle of the jaw with an insertion on the midventral raphe or hyoid. In some species of *Python* it appears to be absent. The *M. constrictor colli* is found in all families of snakes except in the Uropeltidae where it has not been recognized.

3. *M. mylohyoideus anterior*

The superficial *M. mylohyoideus anterior* is generally located ventrally beneath the rami of the lower jaw anterior to the *M. constrictor colli*. It takes its origin from the anterior part of the mandible and inserts on the gular septum.

In *Sphenodon* the *M. mylohyoideus* (*M. intermandibularis* of Rieppel 1978) forms a single large muscular sheet, but in lizards it is differentiated into three sets; the *Mm. mylohyoideus anterior superficialis* (= *M. intermandibularis anterior superficialis*), *mylohyoideus anterior principalis* (= *M. intermandibularis anterior profundus*), and *mylohyoideus anterior profundus* (= *M. intermandibularis posterior*). In some forms, such as *Cabrita*, *Anolis*, *Hemidactylus*, and *Mabuia*, some fibers of the *M. mylohyoideus anterior* originate deep on the medial surface of the mandible and others originate superficially on the *M. geniohyoideus*. As the fibers of the two muscles cross, they break into numerous strips and interdigitate (Figs. 18, 19, and 20).

In turtles the *M. mylohyoideus* is simpler. In *Trionyx* it consists of a single *M. mylohyoideus anterior profundus* that originates

ventral to the M. geniohyoideus from the ventral aspect of the mandible and passes medially to insert on the gular septum. In *Lissemys* the M. mylohyoideus anterior forms as two muscles, with the M. mylohyoideus anterior profundus being identical to that of *Trionyx*. The M. mylohyoideus anterior principalis is a broad sheet originating on the mandible and inserting on the gular septum.

In *Chelodina* and *Deirochelys* the intermandibular series is simple and undivided, originating on the inner surface of the mandible and inserting on the median raphe. In *Chelodina* the anterior quarter of the fibers do not insert into each other as in *Deirochelys*, but are separated by fascia.

Some age variation in this muscle can be seen in *Crocodylus*: in adults the M. mylohyoideus anterior is not distinguishable as a separate muscle, but there are two sheets in the juvenile representing the M. mylohyoideus anterior and mylohyoideus posterior. In adult *Alligator* a single transverse sheet is present (Mm. intermaxillaris and sphincter colli), and in *Gavialis* the one sheet (M. mylohyoideus anterior principalis) is probably homologous to both the Mm. mylohyoideus anterior and mylohyoideus posterior. In *Gavialis* this muscular sheet occupies almost the entire anterior part of the ventral inter-ramal area of the neck, originating on the inner side of the mandible and inserting on the gular septum.

The M. mylohyoideus anterior superficialis exhibits several variations. In *Mabuia* and *Anolis* the fibers extend anteriorly, overlapping the M. mylohyoideus anterior principalis either medially or laterally. In the Chamaeleonidae and Agamidae the Mm. mylohyoideus anterior principalis and mylohyoideus anterior profundus occur together in the form of a double sheet, which we have concluded is a variation of the M. mylohyoideus anterior. In *Varanus*, Sondhi (1958) indicates that the muscle extends transversely from the mental groove to the M. genioGLOSSUS portio major. There are three sets of fibers listed, including a broad M. mentalis superficialis, that originate ventrally, whereas the narrow M. mentalis profundus anterior and the M. mentalis profundus posterior originate dorsally. All three bundles insert in the lining of the buccal floor. These muscles do

not appear to be homologous to the muscular complex we have seen in iguanids and designated the M. mylohyoideus anterior.

In *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, and *Sauromalus* two distinct groups of muscle fibers are found. The M. intermandibularis anterior are deep fibers that originate as a tendon from the coronoid and splenial bones and extend medially on the ventral surface to join at the median raphe, where they interdigitate with about five bundles of the M. geniohyoideus. A small bundle of fibers also extends from the origin to insert on the connective tissue capsule of the sublingual gland. In *Iguana* this muscle forms the bulk of the large dewlap.

The most superficial group of fibers (M. intermandibularis anterior superficialis) is small and narrow, with an origin from the oral membrane and from the anterior part of the M. intermandibularis anterior profundus. The muscle fibers pass obliquely posteriorly to insert on the median raphe. In *Iguana* and *Dipsosaurus* this superficial group is greatly reduced in size.

In snakes the synonymy of the throat musculature is not well established. For this reason we follow rather closely the studies of Langebartel (1968) and Sondhi (1958). The anteriormost set of transverse fibers (M. intermandibularis anterior) is absent in *Anilius* and *Xenopeltis*, but is represented by a tendon in *Rhinophis*. In the anomalepidids, typhlopids, and leptotyphlopids this muscle is broad and may actually represent several muscles. In the latter families one or more muscle groups may originate on the medial surface of the dentary. In the colubrids, viperids, and elapids a single muscle is large but separated into two parts. The longer and thicker anterior one originates on the medial surface of the tip of the dentary and medially to the fibrous inter-ramal pad. The second (posterior) part extends obliquely from the same origin to insert on the ventral raphe. The M. mylohyoideus anterior in *Natrix* (*Xenochrophis*) is probably represented by three muscles: Mm. intermaxillaris, mentalis profundus anterior, and mentalis profundus posterior. The M. intermaxillaris originates from the ventrolateral border of the dentary and passes obliquely posteriorly to insert on the

mental groove. The remaining pair of bundles originate from the mental groove and extend obliquely caudad to insert adjacent to each other on the lining of the buccal floor.

The intermandibularis anterior of *Nerodia* is described as having two separate parts. The M. intermandibularis anterior pars mucosalis has two portions. The first is a small triangular anterior portion that originates on the midventral raphe of the lower jaw and buccal membrane fascia. It inserts on the ventromedial surface of the anterior tip of the dentary and the ligament attached to it. The much stouter posterior slip originates from the midventral raphe of the lower jaw and fascia surrounding the tongue sheath just posterior to the insertion of the anterior slip. The fibers pass anterolaterally to insert on the ventromedial surface of the dentary immediately posterior to the insertion of the anterior slip.

The second part (M. intermandibularis anterior pars glandularis) originates on the midventral raphe of the lower jaw of the fibrous inter-ramal pad. The fibers pass posterolaterally to insert on the ventrolateral side of the sublingual gland at its posterior end. A small number of fibers insert on oral mucosa posterior to the gland.

4. M. mylohyoideus posterior

The M. mylohyoideus posterior is a transverse muscle situated posterior to the M. mylohyoideus anterior.

The M. mylohyoideus posterior [M. mylohyoideus anterior principalis of Sondhi (1958)] of *Trionyx* and *Lissemys* originates from the border of the mandible, where it forms a broad, thick sheet muscle. It extends medially to insert on the gular septum.

In *Alligator*, *Crocodylus*, and *Gavialis* the M. mylohyoideus posterior is represented by a thin sheet that combines into one muscle, the M. mylohyoideus anterior and M. mylohyoideus posterior.

In some lizards (*Mabuia* and *Cabrita*) these muscular sheets are continuous, but show a small division between them. Sondhi (1958) reports that in *Varanus* they are differentiated into two muscles (Mm. mylohyoideus anterior superficialis and mylohyoideus anterior principalis) that are disposed one behind

the other, both originating on the lateral surface of the mandible and inserting on the gular septum.

In the iguanine lizards, an anterior and a posterior sheet of muscle fibers (M. intermandibularis posterior) form the M. mylohyoideus posterior. The anterior sheet is broad and thin, with an origin from the lateral surface of the mandible. The fibers pass medially on each side to insert with their opposite members at the median raphe. The posterior bundle of fibers (about one-quarter of the posteriormost fibers) originate from the lateral surface of the mandible beginning at the midpoint of the retroarticular process and insert on the linea alba.

In most iguanines the M. mylohyoideus posterior exhibits a primitive condition by being continuous with the M. constrictor colli, from which it can be delineated by a natural separation along the entire border only in *Conolophus* and *Ctenosaura*. In *Cyclura* and *Sauromalus* this separation is present only in the medial third of their common border. In *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Dipsosaurus*, *Iguana*, and *Oplurus* the two muscles are continuous along their entire border.

In *Crotaphytus* the Mm. mylohyoidei anterior and posterior form one continuous sheet with no separation between them. In *Phrynosoma* the M. mylohyoideus posterior is separated from the anterior, but is continuous posteriorly with the M. constrictor colli, from which it can be separated only with great care.

In *Eumeces* the position of M. mylohyoideus posterior is similar to that of the iguanid lizards, with both anterior and posterior muscles being separated.

In the teiid *Ameiva* the M. mylohyoideus posterior originates on the medial surface of the dentary and immediately breaks into nine separate divisions that interdigitate with slips of the M. geniohyoideus. It inserts on the midventral raphe just posterior to the M. mylohyoideus anterior (Fig. 17). In *Cnemidophorus* the muscle is as above, except that there are only five divisions instead of the nine in *Ameiva*. The Mm. mylohyoideus posterior and constrictor colli are continuous for their entire border in *Shinisaurus*, but widely separated in *Xenosaurus*.

All snakes except one colubrid (*Amblycephalus kuanungtungensis*) possess a M. mylohyoideus posterior (Langebartel 1968). It lies in the same position as the M. intermandibularis posterior of Langebartel (1968), with the former having its origins on the mandible and insertion on the gular septum. In the colubrid *Achrochordus* it is very broad, attaching to the middle region of the mandible. In *Haplopeltura boa* it is attached lateral to the external adductor muscle of the lower jaw. The fibers are not attached to the mandible, but cross their opposite members at the midventral raphe and interdigitate, eventually attaching to the opposite mandible. M. mylohyoideus inserts on the lingual process in the hydrophid *Aipysurus*.

The second bundle of fibers (M. intermandibularis posterior superficialis) is small and restricted in some snakes with the parallel type of hyoids. Its occurrence is sporadic in colubrids, and it is absent in most poisonous snakes, including the hydrophids. It may be replaced by a tendon that originates from the posterior part of the lower jaw and inserts on the gular septum. Sondhi (1958) states that the M. mylohyoideus posterior is an extremely broad muscle sheet, lying immediately posterior to the M. mylohyoideus anterior and occupying the posterior region of the neck in *Natrix piscator*. He further states that this muscle originates on the dorsolateral surface of the anterior cervical vertebrae and extends ventrally to insert on the posterior part of the gular septum. Langebartel (1968) describes two muscles, a ventral sheet taking its origin from the anterior part of the mandible and extending obliquely anteriorly over the body of the tongue to insert on the gular septum, and a dorsal sheet deep and dorsal to the M. geniohyoideus, with an origin from the mandible with the ventral sheet; the dorsal sheet extends obliquely anteriorly also to insert on the gular septum. The M. ceratmandibularis of Langebartel (1968) occurs in most snakes, although with considerable variation. Because of its location, we include it as a synonym of M. mylohyoideus posterior, even though we are aware that most homologies must yet be proven by careful embryonic study.

The intermandibularis posterior of *Nerodia* is described by Varkey (1979) as having two

slips. The M. intermandibularis posterior pars anterior is the largest of the ventral constrictors originating on the midventral raphe of the lower jaw ventral to the origin of the posterior slip of the intermandibular anterior I and the transversalis branchialis. The origin is broad and thin, passing caudolaterally to form a stout band to insert on the ventromedial surface of the bone at the distal end of the mandibular fossa.

The second slip, which Varkey calls the M. intermandibularis posterior pars posterior, is a thin, flat, triangular sheet of muscle that originates on the midventral raphe posterior to the origin of the intermandibularis posterior I and the transversalis branchialis and the anterior tip of the hyoid cornua. It passes ventral to the M. neurocostomandibularis for most of its length. This insertion is just posterior to the insertion of the pars anterior on the ventrolateral surface of the bone at the level of the proximal end of the mandibular fossa.

5. M. mandibulotrachealis

The M. mandibulotrachealis of *Varanus* has been described by Sondhi (1958) as a delicate muscle arising from the anteroventral part of the mandible and extending posteriorly to divide into two parts. The dorsal part passes posteriorly dorsal to the tongue to insert on the lateral side of the trachea. The ventral part of the muscle extends posteriorly to fan out over the buccal floor near the insertion of the M. genioceratoideus, with an insertion on the ventral lining of the buccal floor. In *Natrix (Xenochrophis)*, Sondhi (1958) found the origin to be similar to that of *Varanus*, with a medial bundle inserting on the trachea and a lateral bundle attaching to the lining of the buccal floor. It has not been reported for other genera.

This muscle is reported by Varkey (1979) for *Nerodia* as the M. geniotrachialis. It is a stout band of muscle that parallels the genioglossus. It originates at the anterior end of the dentary dorsal to the origin of the lateral genioglossus. It passes posteromedially to the tongue sheath and inserts on the ventral and ventrolateral surfaces of the first 14 tracheal rings.

6. *M. neuromandibularis*

The *M. neuromandibularis* has been described in detail by Sondhi (1958) for *Natrix* (*Xenochrophis*) and *Varanus*. In the latter it probably corresponds to the *M. geniolateralis*. Sondhi has described *M. neuromandibularis* as originating from the dorsolateral border of the middorsal aponeurosis and extending a short distance anterior along the dorsal side of the neck. The fibers divide into three sets, which pass into a common tendon inserting on the inner ventral surface of the skin. In *Natrix* (*Xenochrophis*) the origin is similar to that in *Varanus*. The insertion is on the ventromedial side of the posterior half of the mandible.

In some snakes the *M. neuromandibularis* arises from an aponeurosis at the middorsal line. In the anomalepidids, typhlopids, leptotyphlopids, uropeltids, and aniliids it inserts on the lower jaw. In the *Xenopeltidae*, *Boidae*, and other families it inserts on the raphe in common with the *M. ceratomanibularis* and *costomandibularis*.

7. *M. costomandibularis*

The *M. costomandibularis* has been described only for some snakes in which its origin is either from the cartilaginous ribs or the rib cage. In *Thamnophis* a medial slip originates from the peripheral surface of the lining of the pharyngeal floor and inserts on the common tendinous inscription of the *M. neurocostomandibularis*. In *Cylindrophis rufus* the insertion is on the second ceratobranchial as well as on the mandible.

8. *M. constrictor pharyngis*

The *M. constrictor pharyngis* of *Crocodylus* and *Gavialis* is a deeply laid transverse strap apparently restricted to the *Crocodylia*. Its origin is from the lateral surface of the cervical vertebrae and its insertion medial on the gular septum.

9. *M. obliquus abdominis internus*

Langebartel (1968) describes the *M. obliquus abdominis internus* as a trunk muscle

of snakes, with an origin on the medial face of the ribs and an insertion on the linea alba.

10. *M. transverse abdominis*

Langebartel (1968) has also described the *M. transverse abdominis* as restricted to snakes and lying on the deep surface of the *M. obliquus abdominis internus*, with an origin on the medial face of the ribs. After extending posteriorly and medially, it inserts on the linea alba.

VI. THE TONGUE: EXTERNAL MORPHOLOGY

The tongue of reptiles has been investigated by many workers, some of which are as follows: Gräper (1932), Nonoyama (1936), Gnanamuthu (1937), Oelrich (1956), Sondhi (1958), Avery and Tanner (1971), and Kroll (1973). Winokur (1974) published a major study on the adaptive modification of the buccal mucosae in turtles. His study is concerned not only with the tongue, but also with the glands found in the buccal area. Tongues in turtles vary in size and complexity (Fig. 22). Winokur states that

Terrestrial herbivores (*Gopherus*, *Testudo*, and other tortoises) have the best developed mucous glands, whereas aquatic carnivores (*Chelydra* and *Chelus*) have few or no mucous glands.

In both *Chelydra* and *Trionyx* (Fig. 22 A, B) the tongue is without papillae or complex glands and is nonprotrusible, a characteristic of carnivorous chelonians. In *Trionyx* the short, rounded tongue is dorso-ventrally flattened and contains just a base and body. The base is formed from two posterior limbs that they enclose. Each basal portion extends anteromedially to unite in the tongue. Posterior to the tongue and glottis, the buccal-pharyngeal floor has numerous filiform papillae that Girgis (1961) has shown to have a respiratory function. The tongue of some, such as *Chelus*, has been developed as a lure in food-getting: the open mouth exposes a wormlike tongue structure to entice unsuspecting prey into the mouth.

In contrast, the terrestrial herbivorous chelonians (Tortoises; Fig. 22b) have a much

larger lingual pad, which is glandular, fleshy, and somewhat protrusible. Tortoises have profuse lingual mucous glands on and between the lingual papillae as well as muscles capable of some lingual protrusion. They generally lack papillae posterior to the tongue.

Winokur (pers. comm.) considers *Dermatemys* (Fig. 22a) to be a special case. The tongue of this aquatic herbivore shows one end of the spectrum of buccal complexity in aquatic chelonians. Figures 22 and 23 illustrate the extremes seen between the tongues of aquatic carnivorous and terrestrial herbivorous chelonians. The tongue of *Dermatemys*, although proportionately smaller than that of terrestrial *Gopherus*, shows an extreme condition of buccal papillation, but one that is quite different from that of terrestrial herbivorous tortoises. Between these extremes are the majority of chelonians, such as *Pseudemys*, which tend toward omnivorousness.

The tongues of *Alligator*, *Crocodylus*, and *Gavialis* lack any specific areas identifiable as base, body, or apex. The tongue is a mass of tissue between the mandibular symphysis and glottis attached to the lining of the buccal floor except at its anterior tip. It can be elevated and depressed, but not protruded.

Sauromalus (Fig. 24) and *Brachylophus* (Fig. 25) show generalized lizard tongues, with their extensive papillation and lateral extensions on each side of the glottis. Such tongues are protrusible and obviously serve a masticatory function. In *Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, and *Sauromalus* the tongue is well developed and large. In the above genera it is cleft anteriorly, with the most anterior tips lacking papillae. There is a smooth pad ventral to the tips (Fig. 24).

In the teiid *Ameiva* the tongue is rounded and slightly notched posteriorly and covered by a lingual sheath. It bears a deep terminal notch anteriorly that separates the tapering elongate terminal prongs. A lingual sheath is absent in *Cnemidophorus* and other macroteiids. The tongue of *Cnemidophorus* (Fig. 26) represents a moderate advancement in the development of flexibility, and *Chamaeleo* (Fig. 27) is a highly specialized free tongue.

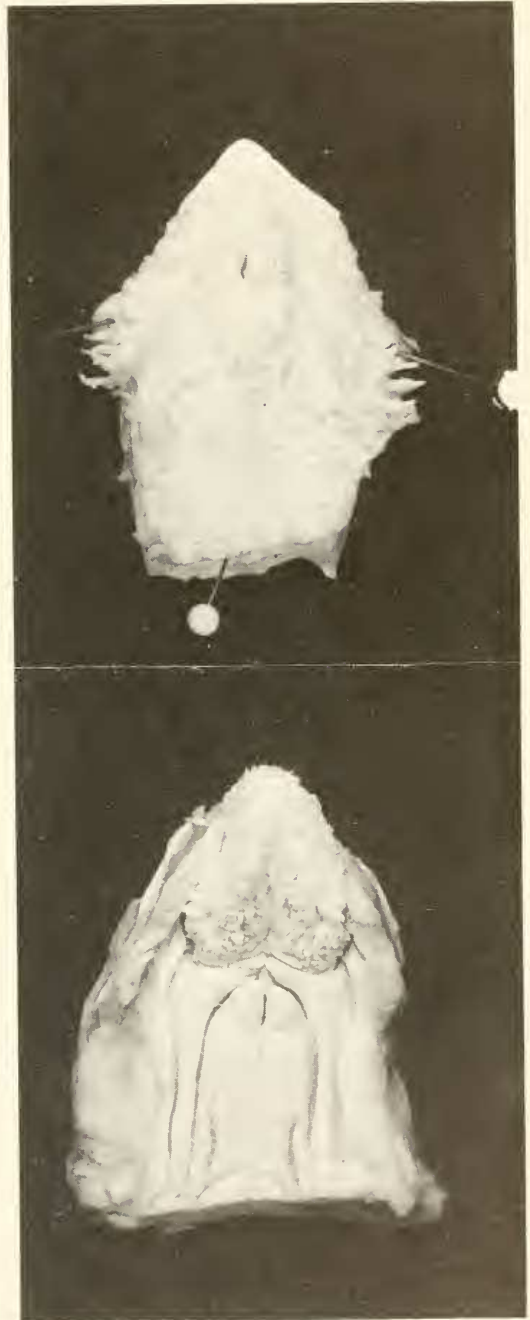


Fig. 22. Tongue size as indicated in: A, *Dermatemys mawi* (UU 9845), above; B, *Gopherus* (UU 5961), below. It should be noted that the glottis is moved caudad as the tongue increases in size. Photographs provided by Robert M. Winokur.

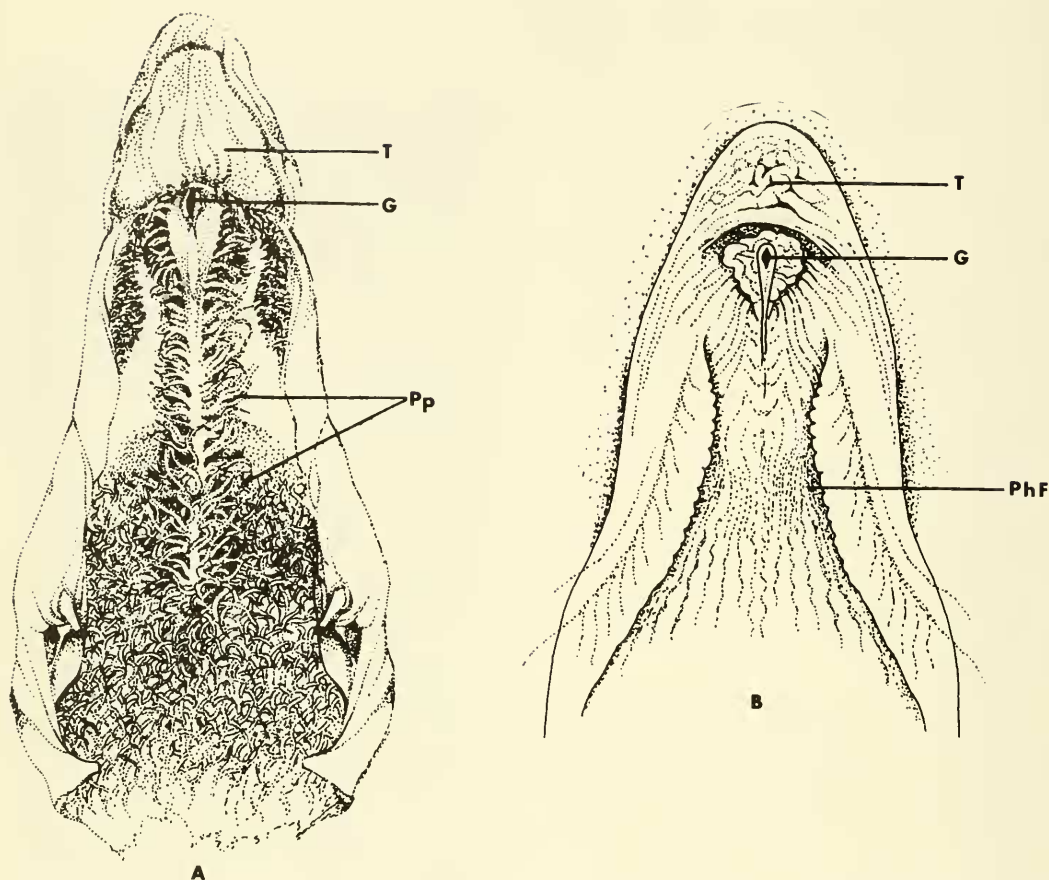


Fig. 23. Tongue of *Trionyx spiniferus*: A, showing its position in relation to the glottis and pharynx area with its filamentous papillae; B, *Chelydra serpentina* showing the nonpapillated pharynx.

In *Lanthanotus* the tongue is deeply incised terminally, forming two tapering prongs. The anterior half of the tongue is elongate, narrow, smooth, and elastic, whereas the posterior half is wide and covered with papillae. In *Shinisaurus* the tongue is similar, but the posterior half is more triangular and the terminal prongs are not as well developed. *Heloderma* has a similar tongue but with proportionately longer terminal prongs than in the latter.

The tongue of *Varanus* is elongated and protrusible, terminating in a forked tip anteriorly. The entire median part of the buccal floor is occupied by its mass. Posteriorly it extends as a bifurcated portion on each side of the glottis and esophagus and into the neck proper. Sondhi (1958) considers the tongue to be divisible into three parts: the base which is bifurcated; the body, formed by

the union of two basal masses of muscle; and lastly the apex, consisting of a pair of prongs. Each muscular mass forming the basal branch of the tongue arises on the distal end of the second ceratobranchial as a slender longitudinal M. hypoglossus, which extends along the ventrolateral surface of each ceratobranchial to pass obliquely to the dorsolateral side of the neck. This muscle eventually occupies a midventral position, with the middle of its basal branch lying ventromedial to the point of articulation between the distal and proximal portions of the second ceratobranchial. Its anterior portion lies ventrolateral to the proximal piece of the anterior cornu at the point of articulation with the basihyoid.

As the two basal branches of the tongue approach, they become thick and sub-cylindrical and eventually lie dorsal to the basihyoid and ventral to the poriones pro-

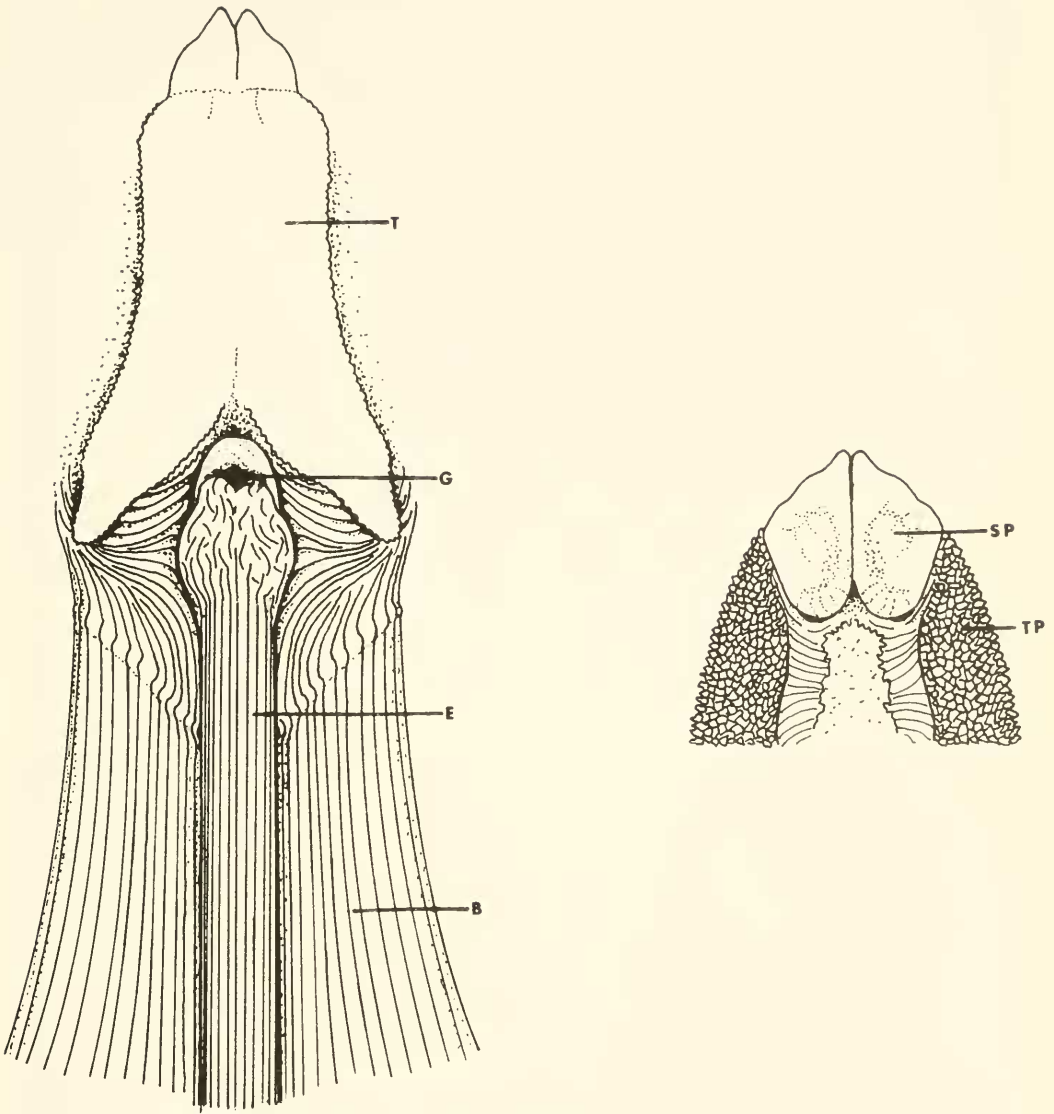


Fig. 24. Tongue of *Sauromalus obesus*: A, outline of dorsal view; B, ventral view showing the smooth pads surrounding the tips. (Dorsal surface as in *Brachylophus*, Fig. 25).

ximales of the anterior cornua. At their anterior extremes the two branches are enclosed in a lingual sheath, where they unite to form the body of the tongue. The body is enclosed by the lingual sheath and occupies the medial area of the buccal floor. Ventrally the anterior end of the lingual process lies inside the lingual sheath and opposite the glottis. Also, ventrally the two handlelike pieces of the porciones proximales overlap medially to cover the body of the tongue. The apex of the tongue consists of a pair of prongs,

rounded, thick at the base, and tapering to pointed ends anteriorly.

We recognize at least three types of saurian tongues. First, in the generalized tongue, seen in such forms as *Sauromalus* and *Coleonyx*, the dorsal surface is papillate and highly glandular; although the tip is divided, it is not extended into a pair of elongated prongs. Second, an elongate, narrow tongue with a pair of elongate prongs occurs in such groups as the teiids and varanids. In these lizards with deeply incised tips, the tongue is narrow

and glandular and serves not only the purpose of mastication, but also functions as a sensory organ. Sondhi (1958) implies that such tongues are closely related anatomically to the tongues of snakes, and he compares the tongue of the natricine snakes to that of *Varanus*. Third, an entirely different tongue is found in *Chamaeleo*. Instead of a further development of the tip as in *Varanus*, the chamaeleonids have developed a blunt end with a highly glandular anterodorsal surface used in capturing and ingesting food.

In snakes the tongue has developed a greater bifurcation with filamentous lateral projections on each fork. Such tongues are sheathed at their base and function as a sensory rather than a masticatory or food-getting

organ. Our understanding of lingual structures and the associated buccal mucosae, however, is still sketchy and much comparative study must be done before an adequate understanding of their anatomy is available.

In *Natrix* (*Xenochrophis*) Sondhi (1958) also describes the tongue as having three parts, with the basal branches lying parallel on each side of the midlongitudinal line ventral to the trachea. Each branch passes anterior to the second ceratobranchial ventromedially. As they approach the dorsal part of the basihyoid, the two branches unite to form the body of the tongue, which is elongated and compressed dorsoventrally. In the retracted position the tongue is almost entirely encased by the lingual sheath dorsal to the basihyoid and lingual process and ventral to the trachea. The apex of the tongue is broad at the base but tapers anteriorly.

The tongue has a variety of forms, sizes, and functions in reptiles. In some aquatic turtles it is a small pad rather tightly applied to the floor of the anterior part of the mouth. Such tongues are nonprotrusible and actually have a very limited ability to move. In most chelonians, except for some aquatic turtles and crocodilians, the tongue is more than a pad and serves many useful functions. In some chelonians (*Gopherus*, Fig. 22b), most lizards (iguanids and agamids for example, Fig. 24), and in the more primitive Sphenodontidae the tongue may serve a masticatory function. It is a "food-getting" organ in the "free"-tongued Chamaeleonidae and has a sensory function in snakes and some lizards.

As noted above, the degree of flexibility in the tongues of reptiles varies from little to considerable movement. Because tongues in most reptiles (except snakes) are associated with feeding, that is, ingestion, their anatomy and perhaps the degree of flexibility is dependent on adaptive change to meet such activities.

In the Sphenodontidae and Chamaeleonidae the extremity is very blunt (Fig. 27). The *Chamaeleo* tongue and its associated muscles and other tissues may be as long or a longer than the body when fully extended. A broad fleshy tongue with smooth and papillate areas is seen in the gekkonids and iguanids (Figs. 24, 25). The Testudines and

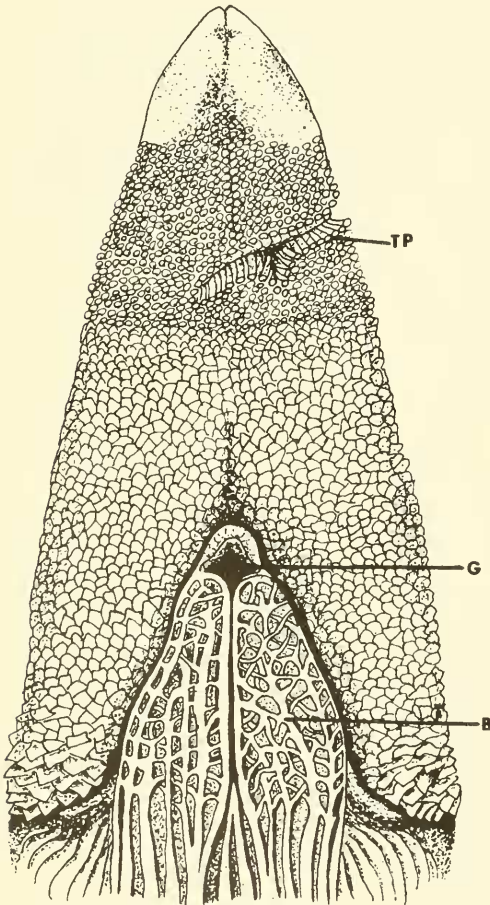


Fig. 25. Tongue of *Brachylophus* showing the size and nature of the tongue papillae (TP), and the reticulated, ridged nature of the tissue (B) extending posterior to the glottis (G).

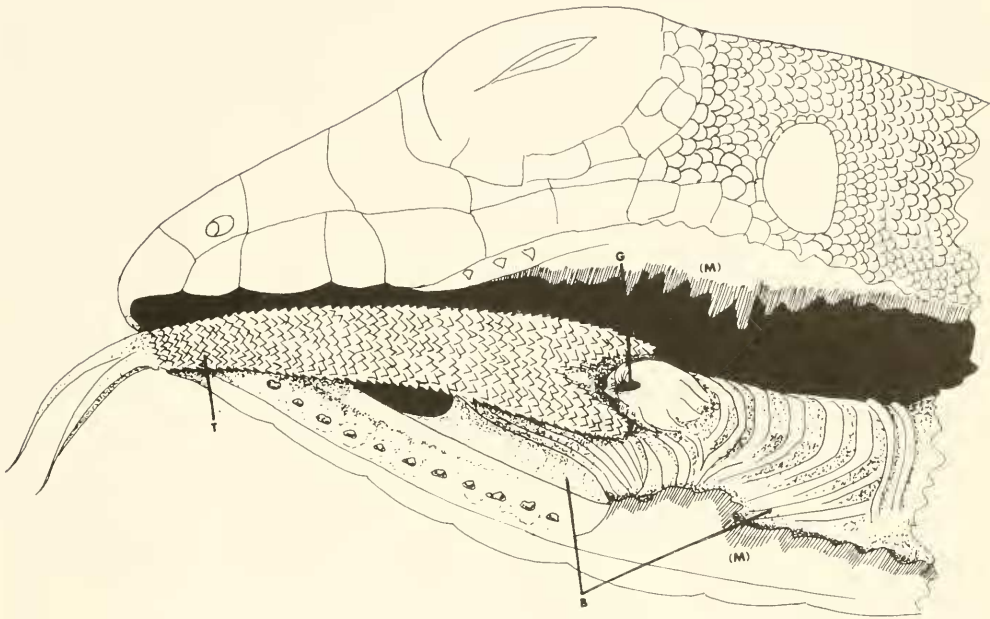


Fig. 26. Dorsolateral view of *Cnemidophorus tigris* (BYU 17366) showing the forked tongue and the narrow papillate body of the tongue (B), floor of the mouth (M), cut muscles.

Crocodilla may have small pads with little movement or, as in those such as *Gopherus*, the tongue is larger, fleshy, and closely tied to the buccal floor and has varying protrusibility.

The highly flexible and protrusible tongue of snakes has become an elongate, slender, sensory organ. In this form it has changed to an entirely different organ than that of most other reptiles, in which the tongue is an organ lying on the buccal floor. In its normal position it is sheathed, with little or none of it visible on the buccal floor. Also, the opening of the tongue sheath has moved anterior so as to lie just posterior to the mental synthesis, with the glottis immediately posterior to the sheath opening. Although ophidian tongues are structurally and functionally quite different from those of most other reptiles, they are nonetheless developed phylogenetically from the same basic structures. The adaptive changes found in the tongues of reptiles are probably some of the most remarkable to be found, for one organ, in the vertebrate series.

VII. MUSCULATURE OF THE TONGUE

The tongue is associated with musculature of two basic types: (1) extrinsic musculature, which does not contribute to the structure of the tongue itself, and (2) intrinsic musculature, which makes up the lingual structures.

1. Extrinsic musculature

In most reptiles the *M. geniohyoideus* is the primary extrinsic muscle of the tongue. It is paired and arises from the mandibular symphysis to insert on the external part of the *M. hypoglossus*, parts of the hyoid apparatus, or the lining of the buccal floor. In *Sphenodon* it has two extensions, one dorsal and one ventral.

In the turtles *Trionyx* and *Lissemys* the *M. geniohyoideus* is undivided and broad. It originates on the mandibular symphysis and extends posteroventrally to insert on the fascia of the ventrolateral border of the body of the tongue.

The *M. geniohyoideus* of *Alligator* takes origin from the mandibular symphysis and di-

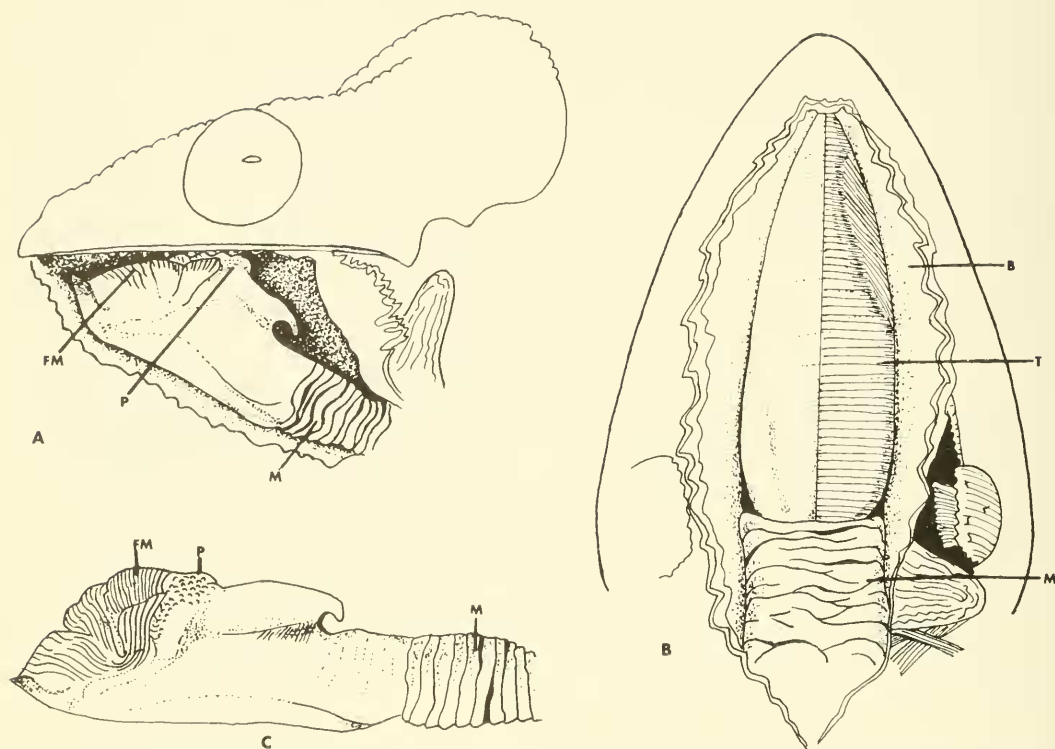


Fig. 27. Tongue of *Chamaelon brevicornis*: A, lateral view showing position of tongue in mouth cavity; B, ventral view with muscles and other tissues removed to show the tongue and the folded M. hypoglossus; C, tongue removed, lateral view (BYU 12422).

vides into medial and lateral bundles. The medial bundle is narrow and interdigitates with its opposite member to insert on the basihyoid. The lateral bundle is broader and inserts on the tongue. The M. geniohyoideus of *Crocodylus* arises from the mandible and divides into two lateral bundles, both of which extend posterodorsal to where the median bundle of the M. geniohyoideus inserts on the anterior border of the hyoid. The lateral bundle inserts on the anterior and ventral border of the anterior cornu. In *Cavialis* the M. geniohyoideus has portiones minor and major, with the portio minor being slender and originating with the mandibular symphysis. It extends caudad to insert on the ventral part of the M. hyoglossus. The broader portio major lies lateral to the M. hypoglossus, takes origin from the mandibular symphysis dorsal to the portio minor, and extends obliquely caudad to a fanlike insertion on the fascia near the middle of the M. hyoglossus (Sondhi 1958).

In *Hemidactylus* the M. geniohyoideus is well developed, with insertions on the ventrolateral surface of the tongue and the hyoid cornu. In *Anolis*, *Sitana*, *Calotes*, and *Draco* the M. geniohyoideus fans out to insert on the buccal floor, with the main body attaching to the sides of the second cornu and the first ceratobranchial. The M. geniohyoideus of *Mabuia* covers the M. hypoglossus on its lateral surface, whereas in *Cabrita* it originates on the medial sides of the mandible. The muscle extends posteriorly to insert on the lining of the buccal floor. In the area of the glottis the main bundles of the M. geniohyoideus divide into two and insert on the first ceratobranchial on the ventral side of the M. hypoglossus.

The M. geniohyoideus of *Chamaeleo brevicornis* consists of two main bundles: the dorsal one inserts on the buccal floor, the ventral one on the body of the hyoid and the first ceratobranchial, lacking any connection with the tongue. The dorsal bundle has three slips

that insert (1) on the side of the pouch in the buccal floor where the tongue retracts, (2) on the buccal floor two-thirds the length of the jaw, and (3) after extending obliquely under the second bundle, on tissue lateral to that bundle.

In *Varanus* the M. geniohyoideus, according to Sondhi (1958), can be divided into two parts. The Mm. geniohyoidei portio minor is very short, extending obliquely posteromedially to insert on the anterior part of the lining of the buccal floor near the midline, and the M. geniohyoideus portio major extends posteriorly for a much longer distance to meet its opposite member at the midline. As the two muscles lie together at the midline ventral to the tongue, each separates into a dorsal and ventral sheet. Each of these divisions insert on the ventral, lateral, and dorsal sides of the tongue to attach on the fascia of the basal branch of the tongue. In *Varanus indicus* the main body of the M. geniohyoideus inserts in a fascia in common with the M. sternohyoideus and to the first ceratobranchial, which lies immediately deep (dorsal) to the fascia.

The M. geniohyoideus of the iguanid lizards *Amblyrhynchus*, *Brachylophus*, *Chalarodon*, *Conolophus*, *Ctenosaura*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Oplurus*, and *Sauromalus* extends posteriorly from the ventromedial surface of the mandibular rami and divides into medial and lateral bundles. The medial bundle passes posteriorly to insert on the ventral surface of the first ceratobranchial. The lateral bundle inserts on the ventrolateral surface of the first ceratobranchial, lateral to the medial bundle. It lies ventral and lateral to the anterior part of the M. hypoglossus. Oelrich (1956), in describing the condition in *Ctenosaura*, states:

The lateral group twists so that at its origin the ventral surface is medial and the dorsal surface is lateral, the most lateral fibers extending dorsally and inserting laterally. The more medial fibers fan out and insert all along the ventrolateral surfaces of the tongue to its posterior end, interdigitating with the dorsal transverse fibers of the intrinsic tongue musculature.

The M. geniohyoideus of snakes is long and slender with one or more heads of origin. In *Liotyphlops* it arises as two heads, but in the Typhlopidae as a group its origin is from the

inter-ramal connective tissue. In the Leptotyphlopidae the origin is by a single head or tendon from the dentary. *Rhinophis* (Uropeltidae) has a medial head originating on the inter-ramal pad, but in *Platyplecturus* only the lateral head is present. *Cylindrophis*, *Sanzinia*, *Enhydris*, *Aipysurus*, and *Bothrops* all possess a M. geniohyoideus with a single head. In most cases the M. geniohyoideus is bound to the tongue by a sheath and extends with the tongue at least to its base. In some forms such as *Liasis*, *Eryx*, and *Xenopeltis* the fibers extend even farther to insert on the M. hyoglossus.

In *Atrretium* the M. geniohyoideus resembles that of *Varanus*, with three divisions: lateral, ventral, and dorsal. Each of these originates on the inter-ramal pad. The lateral division has two bundles, one of which extends dorsolaterally to interdigitate with fibers of the second bundle. Together these bundles insert on the lining of the buccal floor. The ventral division extends posterolaterally to separate into medial, inner, and a lateral bundle in the area of the glottis. The lateral group of fibers cross the medial ventrally to pass medially and to unite with the dorsal division of the M. geniohyoideus. The medial fibers extend posteriorly along the trachea to fan out and insert on the buccal floor, with the main bundle inserting on the trachea itself. The fibers comprising the dorsal division of the M. geniohyoideus extend posteriorly to insert on the lining of the buccal floor. The remainder of the muscle extends posteriorly to join with the lateral bundle of the ventral division and pass parallel to the M. hyoglossus and insert into the tongue as a tendon.

The M. geniohyoideus of *Natrix* arises from the inter-ramal ligament and consists of the M. geniohyoidei portiones minor and major. The portio major consists of fibers similar in configuration to the lateral bundle of the ventral division of *Atrretium*. The medial bundle is not connected to the hyoid and may be a separate muscle, the M. mandibulotrachealis as described in *Natrix* by Sondhi (1958). The portio major is similar to the dorsal division of *Atrretium*, although its fibers do not insert on the buccal floor. The short, slender portio minor extends posteriorly to insert

on the anterior buccal floor. Its origin is adjacent to that of the portio major. The portio major is long, and its fibers converge posteriorly to insert on the base of the tongue.

2. Intrinsic Musculature

The anatomy of the tongue is poorly understood except in a few types that have been studied in detail. Attempts at explaining its morphology in *Ctenosaura* by Oelrich (1956) and *Varanus* and *Natrix* by Sondhi (1958) have only indicated the complexity of this structure in reptiles. The simplest interpretation is that the tongue of reptiles consists of a single muscle, the M. hyoglossus, which has been modified to serve many complex functions.

In the Crocrodilia the tongue lacks the recognizable complex of intrinsic muscles seen in many and is formed from a more simplified association of the fibers of the hyoglossus, which originates on the second ceratobranchials and inserts on the buccal floor. The tongue of *Alligator* has medial fibers of the M. hyoglossus that cross to opposite sides and interdigitate with fibers opposite the muscle. In *Crocodylus* the M. hyoglossus has a triple origin with fibers from the outer proximal part of the second ceratobranchial, the ventral area of the second ceratobranchial at its point of articulation with the basihyoid, and the tendinous sheet where sternohyoid fibers insert on the articulation of the second ceratobranchial with the basihyoid. The tongue of *Cavialis* is described by Sondhi (1958) as having a M. hyoglossus with a double origin. One head originates as a tendon from the middle of the ventral border of the second ceratobranchial, and the second head originates near the point of articulation between the second ceratobranchial and the basihyoid. The M. hyoglossus extends anteromedially with interdigitations of fibers from both sides as the muscle inserts on the lining of the buccal floor.

The tongue of *Lissemys* is formed by a M. hyoglossus consisting of two bundles each originating on the proximal portion of the second ceratobranchials (Gnanamuthu 1937). One bundle inserts on the side of the lingual process, and the other extends anteriorly to divide into two bundles to form the body of

the tongue. In *Trionyx* the M. hyoglossus differs from that of *Lissemys* in that it is a single muscle as in *Varanus* and *Natrix*. The origin is from the ventral surface of the proximal part of the second ceratobranchial in the form of longitudinal fibers. These extend anteriorly and are surrounded by a sheath of connective tissues. As the muscle passes anteriorly, the fibers split into three longitudinal bundles: outer, middle, and internal. This division occurs anterior to the union of the two basal branches of the tongue.

Sondhi (1958) describes the tongue of *Varanus*, using a series of successive transverse sections. To summarize his description, the longitudinal fibers of the M. hyoglossus become oblique and then transverse, with more and more longitudinal fibers changing direction at the periphery of the tongue. The main muscular mass differentiates into two sets of fibers: one peripheral with circular fibers (pars externa) and one inner with longitudinal fibers (pars interna). The two groups are separated by a thin fascial capsule.

The circular fibers of the pars externa become tangential and interweave before the basal branches of the tongue combine at their dorsal borders. At the same time, the fibers in different areas of the pars externa change directions to form three intrinsic muscles: the Mm. verticalis linguae, transversalis linguae, and longitudinalis linguae. The M. verticalis linguae is composed of circular fibers of the pars externa on the inner side of each basal branch of the tongue, which extend vertically to lie between the remaining bundles of the pars externa. The dorsally dispersed fibers of the right and left pars externae become continuous at the union of the two basal branches of the tongue to form the M. transversalis linguae. Posterior to the union of the two basal branches the M. longitudinalis linguae is formed from fibers of the M. transversalis linguae, along the dorsal branch of each half of the tongue, which change their direction from circular to longitudinal. Several bundles of these fibers merge together to form a mass on the dorsolateral side of the tongue, which extends anteriorly to the apex. Just posterior to the anterior bifurcation of the body of the tongue, the pars interna of the M. hyoglossus on each side bifurcates to form two portions, which are separated by

some of the bundles and the *M. verticalis linguae*.

Each prong terminates with the diminishing of the longitudinal and circular bundles and the insertion of their obliquely directed fibers on the epithelium of the tongue.

Natrix (Xenochrophis) has been described by Sondhi (1958) as having a *M. hyoglossus* similar to that of the lizard *Varanus*. In *Natrix* the *M. hyoglossus* envelopes the second ceratobranchial at each side of the origin. Unlike that in *Varanus*, the *M. hyoglossus* of *Natrix* becomes ventromedial to the ceratobranchial and combines with its opposite member far posterior to the basihyoid. The *M. hyoglossus* also divides into parts externa and interna, but in the substance of the tongue rather than at its base as in *Varanus*. A number of longitudinal fibers of the *M. hyoglossus* separate from the rest of the pars externa at the periphery of the tongue to form the partes externa and interna. This change in direction of the fibers is directly associated with the formation of the *Mm. verticalis linguae*, *transversalis linguae*, and *longitudinalis linguae* the same as in *Varanus*. The only difference is that the fibers of the *M. longitudinalis linguae* are formed more anteriorly in the body of the tongue in *Natrix* than in *Varanus*.

Varkey (1979) describes the tongue of *Nerodia cycloprion* as being formed of intrinsic tongue muscles and the *M. hyoglossus*. He describes the *M. hyoglossus* as long, slender, paired retractor muscles making up the bulk of the tongue. They arise from the medial edge of the posterior tips of the ceratobranchials of the hyoid, pass rostrally, laterally, and ventrally to the intrinsic tongue muscles, and are pressed so closely together with them as to be almost indistinguishable. The hyoglossus muscles attach to the hyoid cornua, the tongue sheath, the oral mucosa, the fascia medial, and just posterior to the lateral sublingual glands.

The intrinsic musculature of the tongue of *Lichanura roseofusca* has been described by Hershkovitz (1941) as consisting of five distinct bundles. In the posterior part of the tongue all but the *M. verticalis* are present. The *M. transversus inferioris* forms a sheet on the ventral side of the tongue extending dorsally along the lateral side to meet the ven-

tral extension of the *M. transversus superioris*.

The *M. transversus superioris* occupies most of the dorsal part of the tongue deep to the superficial muscle, the *M. lingualis*, which is restricted to the most dorsal muscular layer of the free, unforked part of the tongue.

The *M. verticalis* forms a midsagittal lingual septum, thin toward the anterior and thick at the posterior end. The fibers of the *M. verticalis* run at right angles to those of the *Mm. t. superioris* and *t. inferioris*. Dorsally its bundles interweave with those of the *M. lingualis*.

The ceratoglossus muscles form a pair of central muscles extending the entire length of the organ and forming most of the cross section of the tongue.

Posterior to the bifurcation of the tongue into terminal prongs, the *Mm. verticalis linguae* and *transversalis linguae* intersect at right angles. Thus, in section the tongue can be divided into four quarters composed of bundles of the *M. longitudinalis linguae* and the pars interna.

At the anterior tip of the tongue, a dorsal and a ventral notch occur medially. The dorsal notch deepens to separate the bases of the terminal prongs. At this point the bundles of the *M. longitudinalis linguae* of each side divide into smaller bundles and intermingle anteriorly toward the tips of the prongs to terminate in the connective tissues of the lingual epithelium (Fig. 26).

The *M. hyoglossus* in *Chamaeleo brevicornis* originates on the tip of the distal end of the first ceratobranchial. A small cartilaginous knob on the end of the ceratobranchial, which appears to be a remnant of the epibranchial, also serves as a point of origin for many fibers. The first and second cornua extend anterolaterally from the basihyal; therefore the *M. hyoglossus*, in its contracted position, extends from its origin medially to the lingual process, where it makes a right angle turn to follow the lingual process into the tongue and to its insertion in the connective tissue surrounding the tongue. Upon reaching the tongue, the *M. hyoglossus* divides into the two sections described by Sondhi (1958) as the pars externa and a medial longitudinal part, the pars interna. A series of circular fibers, which are a part of the sheath,

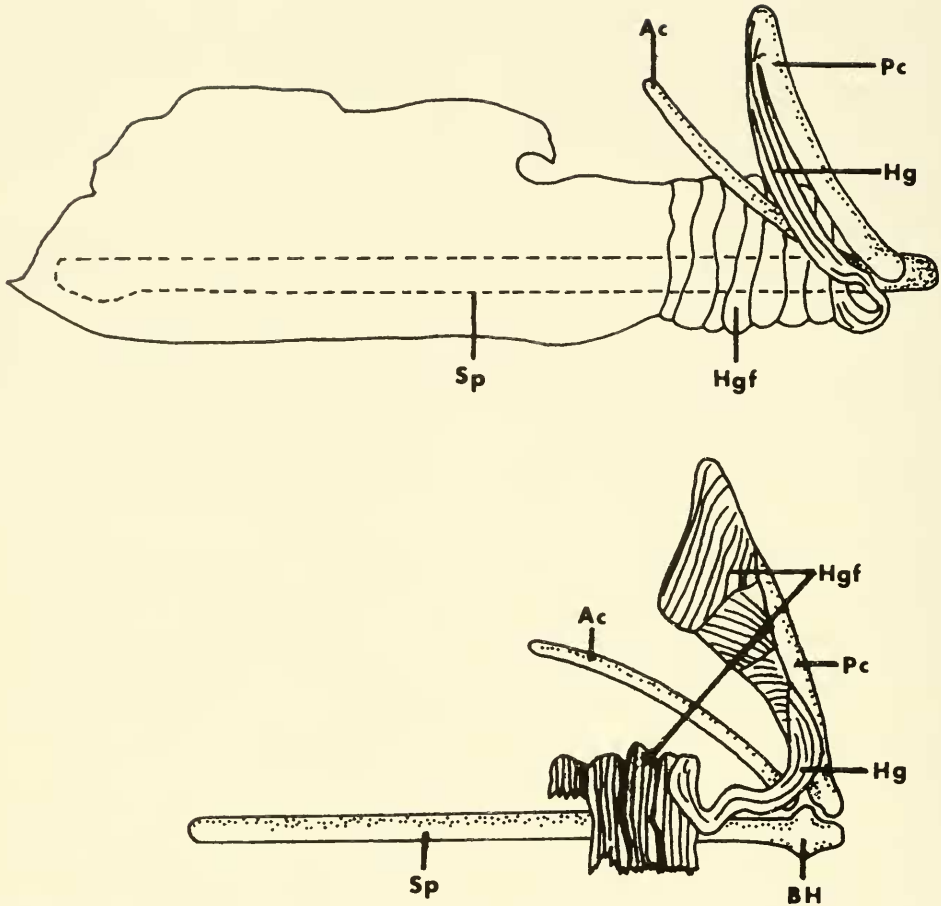


Fig. 28. Lateral view of the tongue of *Chamaelon brevicornis* showing M. hypoglossus from its origin on the posterior cornu to its folds before entering the tongue (BYU 12422).

surrounds the basal part of the tongue as a transverse sheet and encloses the distal lingual process and inserts dorsally into the tongue.

In *Chamaeleo* the M. hypoglossus is folded, less so from its origin to the angle formed at its median posterior than as it extends along the lingual process (Fig. 28). The folds are deep and number 10 before the muscle enters the tongue. When fully extended, this folded part becomes an elongate, slender shaft supporting the clublike tongue. Gnanamuthu (1930) described the anatomy and function of the hyoid apparatus and tongue in *Chamaeleo caccaratus*. His figures 5 and 6 correspond closely to our findings in *Chamaeleo brevicornis*. The folding is similar to the folds in the bellows of an accordion, whereas the muscular folds in free-tongued plethodontid

salamanders is a series of looped folds (Tanner 1952).

The outer bundle further divides into five to six smaller bundles, which lie beneath the dorsolateral border of the tongue to form the M. longitudinalis linguae. The fibers of the upper dorsolateral bundles of the M. longitudinalis linguae extend anteriorly to become obliquely transverse and give rise to the M. transversalis linguae, with the lower bundles continuing longitudinally to merge with each other. The internal longitudinal fibers of the M. hypoglossus become compact and vertical to form the M. verticalis linguae, just behind the tip of the tongue. At that point the middle bundle, between the Mm. transversalis linguae and verticalis linguae, passes dorsally so as to lie above the latter two bands. In the terminal end of each muscular

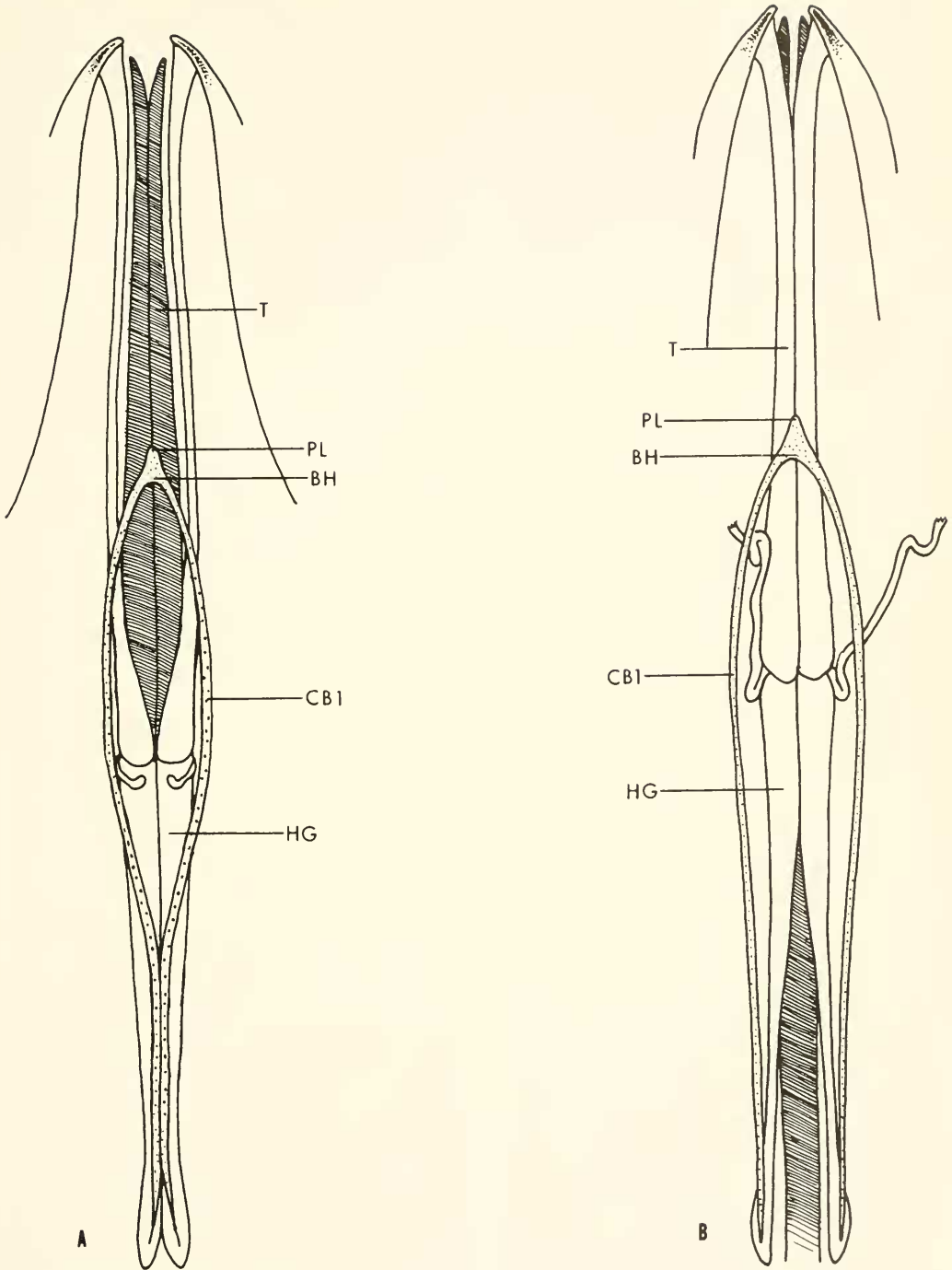


Fig. 29. Ventral view of hyoid apparatus and associated structures: A, *Crotalus v. lutosus*; B, *Pituophis m. deserticola*. HG—m. hyoglossus, t—tongue.

prong extending into the tongue from each side, the various bundles dwindle and insert in the subepithelial connective tissue of the tongue.

In Figure 29 the general structural relationships of the hyoid, tongue and *M. hyoglossus* are depicted for the genera *Crotalus* and *Pituophis*.

In summary, the intrinsic muscles of the tongue are actually fibers of the hyoglossal muscles that extend in varying directions. Unfortunately, the remainder of our knowledge of the tongue and related structures is incomplete. Many structures such as lingual glands, glottis, trachea, and their associated muscles and nerves have not been fully investigated in all groups. Zug (1971) has studied the arterial patterns in iguanids, Winokur (1974) has studied the buccal mucosae in turtles, and Schumacher (1973) has examined the hyolaryngeal muscles and skeleton in turtles and crocodilians.

VIII. INNERVATION OF BUCCAL FLOOR MUSCULATURE

A. General

The innervation of muscles in reptiles has been generally neglected, and for this reason it is difficult to homologize their detailed musculature. Detailed descriptions of the nerve patterns in the buccal floor of reptiles are available from the following workers: Osawa (1898), Watkinson (1906), Reese (1915), Willard (1915), Poglayen-Neuwall (1953, 1954), Oelrich (1956), Schumacher (1956, 1973), Sondhi (1958), and Rieppel (1978, 1981). Soliman (1964) describes and figures the nerves in the head of *Chelydra serpentina* and provides colored plates depicting the nerves entering the muscles associated with the buccal floor and the tongue. Islam (1955) and Islam and Ashig (1972) describe the cranium and cranial nerves of *Uromastyx hardwicki*, and Renous-Lecru (1972) discusses the branchial plexus in *Agama* and *Chalarodon*.

All these workers indicate that in reptiles the IXth (glossopharyngeal), Xth (vagus), XIth (spinal accessory), and XIIth (hyoglossal) cranial nerves usually occur in close association and form a glossohyoidean plexus. Some uniformity does exist in the innervation of the throat muscles of reptiles, as demonstrated by the fact that in all reptiles the Vth (trigeminal) cranial nerve innervates the M. mylohyoideus anterior, the VIIth (facial) innervates the Mm. mylohyoideus posterior and constrictor colli, and the XIIth (hypoglossal) and anterior spinal nerves innervate the M. constrictor colli.

B. Cranial Nerves

Oelrich (1956) presented a clear picture of the pattern of cranial nerves in the iguanid *Ctenosaura*. He found the following nerves innervating muscles of the buccal floor. A similar pattern in all cases has been described for *Anolis* by Willard (1915), for the trigeminal in turtles by Poglayen-Neuwall (1953), and for *Varanus* by Watkinson (1906).

1. *N. trigeminus*: A branch of the trigeminal nerve (ramus ad musculus mylohyoideum) passes through the posterior mylohyoid foramen to enter the lateral fibers of the first mandibulohyoid muscle and terminates anteriorly on the M. intermandibularis posterior. A second branch, the anterior mylohyoid nerve, emerges on the medial side of the mandible from the anterior mylohyoid foramen of the splenial bone to pass over the M. mandibulohyoideus I to enter the ventral surface of the M. intermandibularis anterior. A section of the mandibular ramus continues anteriorly to the lingual ramus of the hypoglossal nerve, where the latter passes through the anterior inferior alveolus foramen of the dentary to divide into two branches. The anterior glandular branch passes the ventral surface of the M. intermandibularis anterior, whereas the posterior branch enters the Mm. intermandibularis anterior and genioglossus.

2. *N. facialis*: The facial nerve divides into a hyoid ramus that innervates a part of the M. intermandibularis that inserts on the retroarticular process of the mandible. It also innervates the M. constrictor colli and the posterior border of the M. intermandibularis.

3. *N. glossopharyngealis*: The M. hyoglossus is innervated by a ramus formed from branches of the glossopharyngeal and hypoglossal nerves.

4. *N. hypoglossalis*: There are four small ventral branches of the hypoglossal nerve that innervate the M. mandibulohyoideus I. The hypoglossal divides into three main branches at the point where the Mm. genioglossus and hyoglossus join. These branches include the ramus lingualis lateralis, which extends anterolaterally to enter the insertion of the M. genioglossus and medial and lateral areas of the M. genioglossus. It next emerges to join the lingual ramus of the trigeminal

nerve, which then enters the tongue. The remaining two branches, intermedialis and medialis, go directly to the tongue, where they innervate its musculature.

Watkinson (1906) described the nerve patterns seen in *Varanus* and found the following:

a. *N. trigeminus*: There are three main branches of the trigeminal nerve (rami ophthalmicus, maxillaris, and mandibularis); however, only the ramus mandibularis goes to the buccal floor, where it has three branches.

The first branch, the ramus ad musculus mylohyoideus, originates from that part of the ramus mandibularis (portio alveolaris inferior) that lies within the alveolar surface of the dentary. It emerges to proceed posteriorly, with branches going to the Mm. mylohyoidei posterior as profundus and superficialis.

The second branch, the ramus muscularis et glandularis, also arises from the portio alveolaris inferior of the mandibular ramus. A branch extends to the Mm. mentalis superficialis, mentalis profundus anterior, and mentalis profundus posterior. It also enters the portiones major and minor of the M. genioglossus.

A third branch, the ramus lingualis, originates from the ramus mandibularis before the latter enters the alveolar canal. This branch emerges from the canal to pass along the ventral buccal floor, where it joins the ramus lingualis anterior of the hypoglossal nerve. It enters the lingual sheath and then the tongue, extending to the anteriormost extremity of the terminal prongs to innervate, with the hypoglossal nerve, the bundles of the M. hyoglossus.

2. *N. facialis*: The facial nerve emerges from the cranium and divides into an anterior branch, the ramus palatinus, and a posterior branch, the ramus hyomandibularis. The latter branch extends posteriorly as the ramus hyoideus to innervate the Mm. geniolateralis and constrictor colli.

3. *N. hypoglossus*: The hypoglossal nerve extends obliquely posterior along the dorsal side of the neck to the buccal floor, where it divides into two branches, each of which further subdivides into two branches. One branch forms the rami ad musculus geniotrachealis,

and the second branch gives rise to the rami linguales anterior and posterior.

The ramus ad musculus geniohyoideus extends obliquely over the M. ceratohyoideus to form two branches that innervate the mid-dorsal region of the M. geniohyoideus and lateral surface of the M. constrictor colli, respectively.

The ramus ad musculus ceratohyoideus et musculus mandibulotrachealis extends from the M. interportalis to the M. ceratohyoideus, innervating these and also sending branches to the Mm. cornuohyoideus and mandibulotrachealis.

The third branch (ramus lingualis anterior) originates from the hypoglossal nerve and extends along the lateral border of the tongue to eventually anastomose with the ramus lingualis of the mandibular ramus of the trigeminal nerve. As it does so, it sends branches to the sublingual glands and terminates in the M. genioglossus. A small branch also extends to both the Mm. genioceratoideus and mandibuloproximalis.

The ramus ad musculus mandibulohyoideus is derived from the hypoglossal nerve before the branching of the ramus lingualis posterior. It innervates the M. mandibulohyoideus.

Two other branches derived from the hypoglossal (lingual accessorii) innervate the posterior part of the base of the tongue. A final branch, the ramus lingualis posterior, is the terminal portion of the hypoglossal nerve. It also innervates the basal area of the tongue.

Some information is available for other lizards such as *Chamaeleo* and *Calotes* (Gnanamuthu 1937), in which the formation of the lingual nerve varies. The lingual branch of the hypoglossal in *Chamaeleo* is separated from the glossohyoidean plexus and forms two branches, the rami linguales lateralis and medialis. The ramus lingualis lateralis extends posteriorly to innervate the M. genioglossus, and the main branch anastomoses with the lingual branch of the Vth cranial nerve; together they penetrate the M. hyoglossus and join the ramus lingualis medialis that enters and innervates the M. hyoglossus. This same branch in the anterior region of the buccal floor unites with the combined lingual branch and with it also enters the tongue. In

Calotes the lingual branch of the hyoglossal nerve extends one branch to the M. genioglossus and one to the tongue. The main branch unites with a ramus of the trigeminal to penetrate the tongue and there subdivides into many branches for innervation of the tongue muscles.

Sondhi (1958) gives the following nerve pattern for the buccal floor of *Natrix* (*Xenochrophis*), a natricid snake:

1. *N. trigeminus*: The ramus mandibularis of the trigeminal nerve sends three branches to the buccal floor. The first branch (ramus ad musculus mylohyoideum) originates from the mandibular ramus immediately after the latter enters the alveolar canal of the dentary as the portio alveolaris inferior. It divides into two branches, one innervating the M. mylohyoideus posterior profundus and the other the M. mylohyoideus posterior.

A second branch, the ramus muscularis et glandularis, originates from the portio alveolaris inferior of the mandibular ramus. After emerging from the mandible, it extends medially to provide branches for the Mm. intermaxillaris, genioglossus portio major, mentalis profundus anterior, and mentalis profundus posterior.

The third branch (ramus lingualis) arises from the portio alveolaris inferior of the mandibular ramus after the mandibularis et glandularis. It unites with the ramus lingualis of the hyoglossal nerve and extends medially to the lingual sheath and M. hyoglossus.

2. *N. facialis*: The facial nerve emerges from the foramen prooticum and extends to the M. mylohyoideus posterior as the ramus hyomandibularis, which has two branches to that muscle.

3. *N. hypoglossal*: The hypoglossal nerve has three main branches, including the ramus descendens that originates as a thin branch extending posteromedially to innervate the ventral surface of the Mm. omohyoideus, sternohyoideus, and sternothyroideus.

The second branch is the main stem of the hypoglossal nerve, which forms the ramus lingualis posterior. It extends forward as two branches, one entering the body and the other the base of the tongue.

The third branch, the ramus ad musculus geniolateralis, originates in the hypoglossal nerve almost opposite the ramus lingualis

posterior and innervates the M. geniolateralis. Distally the hypoglossal bifurcates into two branches, an inner ramus ad musculus mandibulotrachealis and an outer ramus ad musculus geniohyoideum. The inner division extends anteriorly and medially to innervate the posterior part of the M. mandibulotrachealis. The outer branch extends anterolaterally to form two branches that innervate the M. geniohyoideus.

Langebartel (1968) has summarized the innervation of the muscles of the buccal floor in other snakes. The mandibular division of the trigeminal nerve innervates the M. intermandibularis and parts of the tongue. The facial innervates part of the Mm. constrictor colli and the cervicomandibularis and sends some branches to the tongue. Some branches from glossopharyngeal and the vagus innervate the M. ceratomandibularis, but only one branch innervates the M. hyotrachealis. The hypoglossal nerve innervates the Mm. geniohyoideus, ceratomandibularis, and sternohyoideus. The Mm. genioglossus and hypoglossus are innervated by an anterior branch of the hypoglossal nerve. Very commonly the glossopharyngeal, vagus, and hypoglossal nerves combine to innervate the lingual sheath and the Mm. genioglossus and hypoglossus. The hypoglossal may also have anterior and posterior branches that enter the tongue. Last, an anterior branch of the hypoglossal unites with a branch of the trigeminal to innervate the Mm. genioglossus and geniotrachealis. Varkey (1979) describes the innervation of muscles in *Nerodia*, but does not attempt to identify the nerves.

Soliman (1964) describes and figures the cranial nerves of *Chelydra serpentina*. Colored plates depict the various nerves entering the muscles associated with the buccal floor and the tongue.

Trionyx has been described by Sondhi (1958), who indicates the existence of the following nerve pattern, comparable to that reported for *Chelydra*:

1. *N. trigeminus*: The mandibular ramus of the trigeminal nerve has two branches, including the ramus ad musculus mylohyoideum that arises in *Varanus* and *Natrix*, and the ramus lingualis. The former branch extends posteriorly along the medial side of the mandible to divide into two branches, one of

which innervates the *M. mylohyoideus* anterior and the other which innervates the *M. mylohyoideus* posterior. The ramus lingualis arises from the portio alveolaris inferior and emerges from the mandible through a small foramen to innervate the *M. genioglossus*. Soliman and Hegazy (1971) also describe this nerve in *Chalcides ocellatus*.

2. *N. facialis*: The facial gives rise to the ramus hyomandibularis, which innervates the buccal floor. It extends posteriorly as the ramus digastricus and sends a branch to the *M. constrictor colli* and another to the *M. constrictor superficialis*.

3. *N. hypoglossus*: The hypoglossal nerve extends along the anterior part of the neck to the *M. ceratohyoideus*, where it gives rise to two branches, the rami descendens and ad musculus sternothyroideum. A third branch (ramus ad musculus geniohyoideum) is formed as it emerges on the ventral side of the *M. ceratohyoideus*. Finally, it extends anteriorly to provide the ramus lingualis and then terminates by dividing into two branches, the rami ad musculus entoglossohypoglossalis and ad musculus hypoglossolateralis.

The ramus descendens extends anteromedially beyond the second ceratobranchial to form two branches that innervate, respectively, the *Mm. omohyoideus* and the *sternohyoideus*. The ramus ad musculus sternothyroideum extends across the surface of the *Mm. omohyoideus* and *sternohyoideus* to innervate the *M. sternothyroideus*. The ramus ad musculus ceratohyoideus extends to the dorsal surface of the *M. ceratohyoideus*, which it innervates. The ramus ad musculus mandibulohyoideum is a small branch extending anteriorly to innervate the ventral surface of the *M. mandibulohyoideus*. The ramus ad musculus geniohyoideum extends anteriorly to form two branches, with one innervating the portio ventralis and the other entering the portio distalis of the *M. geniohyoideus*. The ramus lingualis extends medially to enter the base of the tongue, where it passes anteriorly inside the tongue to innervate the *M. hyoglossus*. As in *Lissemys*, there are no anastomoses with the lingual branch of the trigeminal. The ramus ad musculus entoglossohypoglossalis is a delicate

branch innervating the *M. entoglossohypoglossalis*. Finally, the ramus ad musculus hypoglossolateralis extends obliquely lateral to innervate the *M. hypoglossolateralis*.

Sondhi (1958) has investigated the nerve patterns of the buccal floor seen in *Cavialis* and presents the following pattern.

1. *N. trigeminus*: The mandibular ramus of the trigeminal nerve forms two branches, the rami ad musculus mylohyoideum and lingualis. The former emerges from the dentary and passes posteriorly to innervate the dorsal surface of the *M. constrictor colli*. The ramus lingualis emerges from a foramen after arising from the portio alveolaris inferior. It passes obliquely anterior to innervate the *M. genioglossus portio major*.

2. *N. facialis*: The ramus hyomandibularis of the facial nerve sends a branch, the ramus hyoideus digastricus, of Sondhi, posterior to the neck to divide into two branches. The first branch innervates the *M. constrictor pharyngis* and the second extends dorsally to the *Mm. constrictor colli* and *constrictor superficialis*.

3. *N. hypoglossus*: On the dorsal side of the neck the hypoglossal nerve divides into four branches. The first branch, or ramus descendens, divides into two branches at or near the middle of the *M. omohyoideus*. These branches innervate the *M. omohyoideus* and the *M. sternohyoideus*, respectively. The second branch, ramus ad musculus sternohyoideum, passes obliquely posterior to divide into several branches that innervate the *M. sternohyoideus*. The ramus lingualis posterior forms the third branch and sends a subdivision, the ramus ad musculus geniohyoideum, to the *M. geniohyoideus*, and other branches enter the tongue and innervate the *M. geniohyoideus portio major*. The last branch, ramus lingualis anterior, extends posteriorly to the mandible to innervate the *Mm. ceratohyoideus* and *mandibulohyoideus*, and other branches extend anteriorly to enter the tongue and the *Mm. genioglossi portiones minor* and *major*.

Reese (1915) indicates that the ramus mandibularis (ramus maxillaris inferior of Reese) of the crocodile divides into two and then four branches. Two of these branches in nerve the *M. mylohyoideus*. The *M. hyoglossus* is served by branches of the IXth and XIIth

nerves. The hypoglossal nerve also sends branches to the Mm. omohyoideus, sternohyoideus, geniohyoideus and genioglossus.

B. Spinal Nerves

Oelrich (1956) reports that in *Ctenosaura* the first spinal nerve innervates the ventral part of the M. omohyoideus and the dorsal part of the sternohyoideus. Sondhi (1958) indicates that in *Varanus* and *Natrix* the united stems of the first and second spinal nerves anastomose with the hypoglossal nerve and extend posteriorly in the neck to send small branches to the Mm. sternohyoideus and sternothyroideus and a large branch to the M. omohyoideus. Some of the succeeding spinal nerves also innervate the M. constrictor colli.

In *Natrix*, as in *Varanus*, the first and second spinal nerves innervate parts of the M. constrictor colli. In some other snakes many spinal nerves innervate the Mm. neuromanibularis, costomandibularis, costo-cutanei inferior and superior, omohyoideus, sternohyoideus, and transversus branchialis.

In *Trionyx*, *Gavialis*, and *Crocodylus* the united stem of the first and second spinal nerves innervates the M. constrictor colli, whereas in *Crocodylus* numerous branches of first, second, and third spinal nerves innervate the smaller ventral muscles of the neck.

IX. DISCUSSION

An examination of the preceding descriptions show that the information on the hyoid and associated structures was widely scattered and incomplete. Although morphology is one of the oldest branches of biology, there is an absence of complete accounts of the gross anatomy of the buccal floor of reptiles as a class. Similar gaps in our knowledge exist for other anatomical areas of the reptilian body. In spite of our acceptance of some reptilian ancestral stocks as being the lines of descent for birds and mammals, anatomists have not vigorously pursued studies to show phylogenetic relationships. The lack of a complete understanding of these groups is astounding considering the important phylogenetic position of reptiles.

Despite the lack of information, some generalizations can be made. As indicated by Sondhi (1958), the buccal floor in many reptiles has three functions: (1) it participates in the act of inspiration and expiration, (2) it aids in the capture and the deglutition of food, and (3) it provides the mechanisms of tongue movement. To Sondhi's list should be added two additional functions: (4) behavioral display and (5) sensory reception.

The important role of the buccal area as a respiratory throat pump has been explored by Gnanamuthu (1937), who demonstrated the part played in *Hemidactylus*. He states,

The contraction of the thorax expelling air would result in the inflation of the buccal cavity, and when next the thorax relaxes this impure air may be taken into the lungs again, because the thoracic contraction and expansion follows each other so rapidly. However, the elevation of the mouth floor and tongue through the aid of transverse and hyoid muscles just when the thorax contracts serves to expel the vitiated air effectively out of the body.

Respiratory mechanisms in reptiles vary widely. *Calotes* utilizes the limbs of the anterior cornua and the attached muscles to actively raise and lower the throat. The positions of cornua and ceratobranchials and associated muscles in *Varanus* indicate a change of the volume of the throat caused by dilation and compression of the floor of the mouth.

Among the testudines, the posterior part of the M. hyoglossus and the entire Mm. ceratohyoideus, entoglossohypoglossalis, and hypoglossolateralis utilize the jointed basihyoid and hypoglossum to move the throat up and down as one solid piece. Although these structures may not be important in respiration (Mitchell and Morehouse 1863), there is reason to believe that both aquatic and terrestrial turtles pump the throat to exchange water and air in the nasal canals and buccal cavity for sensory functions (McCutcheon 1943). In Figure 19 we attempt to reproduce the extensive fimbriations on the buccopharyngeal floor of *Trionyx*. The total function of these numerous filaments may not be fully understood, but seemingly they are important in aquatic respiration (Girgis 1961).

In snakes, inspiration and expiration are accomplished by the muscles of the body wall compressing the lungs for expiration and

expanding for inspiration. A minor contribution is made by the expansion and contraction of the anterior part of the body. As a result, the hyoid has become greatly reduced and contributes mostly as a support for the buccal floor and as a support for the muscles and membranes that open and close the glottis. For further information on respiration in vertebrates, see Hughes (1963), Gans and Hughes (1967), Bishop and Foxon (1968), and Gans (1969).

Food capture and deglutition in reptiles is difficult to correlate with the morphology of the buccal floor. For example, snakes have a ligamentous connection between the mandibular rami and movable articulations of the maxilla, palatine, pterygoid, and quadrate, which allow for the movement of one side of the jaw apparatus to move forward and secure a firm hold on the prey before moving the other side, as indicated by Gans (1961) and Frazzetta (1966). Such a situation does not exist in the Lacertilia, Amphisbaenia, Rhychocephalia, Testudines, or Crocodylia, making comparisons difficult, if not impossible. In the latter three groups, however, the food capturing and swallowing mechanisms are basically similar owing to the greater similarity of throat anatomy.

The movement of the tongue is important in most reptiles because of its sensory nature and association with Jacobson's organ. The tongue is simplest in the primitive testudines and Crocodylia, indicating a more ancient and conservative nature in these groups. The primitive lizards, such as iguanids, and some testudines, such as *Gopherus*, have a thick, fleshy tongue, used both for sensory activities and manipulation of the food within the mouth (Avery and Tanner, 1971; Gnana-muthu, 1937). An advanced lizards, such as *Varanus*, the tongue is similar to that of snakes in gross morphology. The fact that the associated throat musculature in these two groups differs is an indication that perhaps the manipulation of the tongue in varanids and snakes has been, at least partially if not completely, freed from the buccal floor musculature.

Last, the buccal floor has behavioral implications in many lizards, particularly the iguanids, in which males often have enlarged throat dewlaps. The behavioral implications

of these structures is beyond the scope of this paper [see work of Carpenter 1965 (*Anolis*), 1967, 1977 (Iguanids), 1970 (Agamids)], but in the forms with the best developed dewlaps, such as *Anolis* and *Iguana*, the second ceratobranchials and associated musculature provide the main structural components of movement.

Some generalizations about the buccal floor can also be made. The more primitive the organism, the less complicated and specialized the gross anatomy of the buccal floor. This is apparently true for most orders, although there are exceptions within some orders (such as in some testudines). In the primitive forms, the hyoid has retained more cornua, some specialized muscles are absent, and the tongue is less differentiated. In the more advanced forms, such as lizards, the hyoid has become complex and the musculature has proliferated and specialized.

Lizards show a greater variation in the morphology and function of the tongue than do other groups of reptiles. Tongues are structured for food manipulation (Iguanidae and Amphisbaenia), food getting (Chamaeleonidae and Amphisbaenia), and also for sensory functions in such groups as *Cnemidophorus*, *Heloderma*, and *Varanus*. Such functional variations have in turn altered the basic morphology of the buccal floor to accommodate the adaptive feeding habits and the associated sensory and behavioral activities. In snakes specializations of feeding and life habits have caused a secondary reduction of many elements of the buccal floor, particularly in the skeletal structures, and the tongue is no longer a manipulator of food. In snakes the tongue is filamentous and important primarily as a sense organ. As indicated by Sondhi (1958), there is a structural similarity between the tongues of some lizards (*Varanus*) and snakes. This, Sondhi reasoned, may have led to the development of the highly sensitive tongues of snakes. At least, such lizards have a flexible tongue and the terminal forking is structurally similar enough to suggest an evolutionary relationship. Perhaps this is an example of convergence of structure to perform a similar function in distantly related groups.

In general it is difficult to draw major phylogenetic conclusions from the buccal floor

because the scope of such a study is necessarily limited to one specialized area and can be misleading. When hyoid elements are lost, the associated muscles are also lost or may become unrecognizable. Thus the implication of presence or absence of structures is also misleading. Future morphological phylogenetic studies in the area of the buccal floor should be supplemented by embryological information, as indicated by DeBeer (1930, 1951) and Edgeworth (1935). Such research will provide clues as to which structures have been lost, fused, readapted or never possessed by an organism.

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We have used freely skeletal and dissected material used in previous studies at our laboratories. These have served us not only as source materials, but also for the comparative studies.

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In the preparation of this study we have relied heavily on the studies of Gnanamuthu (1937), Langebartel (1968), and Sondhi (1958). Because these are basic studies dealing in some detail with the buccal area, we refer to them repeatedly. Without them this study would have been extremely difficult.

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